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Biological traits as functional indicators to assess and predict (using statistical models) the status of different habitats

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SUMMARY

One of the most widespread yet manageable pressures imposed on the seabed is that resulting from disturbance of the substrate by towed demersal fishing gear (bottom fishing and dredging). Demersal fishing gears are deployed on every continental shelf in the world and, in UK waters, the footprint of fishing is estimated to account for over 99% of the known footprint of all human pressures on the seabed. It is, therefore, essential that current and future management of fishing activities are based on an improved scientific rationale in order to improve the long-term sustainability of this activity.

While the impacts of demersal fishing on the biological characteristics of the seabed have been well-studied, the approaches have tended to focus on assessing impacts on the structural (e.g. changes in species composition, diversity, etc.) characteristics of seabed biological assemblages. However, it is being increasingly appreciated that observing changes solely in the structural attributes of benthic assemblages provides only a limited capacity to inform us of the implications for, arguably far more important, ecosystem function. The present study aims to bridge this knowledge gap by analysing data regarding the biological assemblages of a large number of stations covering a range of habitats across the European continental shelf. We perform this using a biological traits analysis (BTA) in which the assemblages, and the differences between them, are quantified by their relative differences in the morphological, behavioural and life history characteristics of their individuals, as opposed to their taxonomic (i.e., based on species identity) differences. This BTA approach affords the opportunity to understand the potential differences in ecological functioning due to fishing impacts, beyond that which would otherwise be possible from structural approaches.

Traits data regarding the infauna (those organisms that live within the sediment) were available for 819 sampling stations, while for the epifauna (those living on the sediment), data for 1316 stations were analysed. BTA was undertaken on these two biological components independently. The infaunal stations were categorised into 13 EUNIS habitats (level 4) while the epifaunal data represented seven EUNIS (level 3) habitats. Additionally, the data for the infaunal stations were classed according to habitats that were derived following a k-means clustering approach of the environmental characteristics; this allowed an assessment (for the infauna) of the importance of using different habitat derivation methods for biological traits assessments over large spatial scales.

Using data from relatively non-fished stations, fuzzy correspondence analysis (FCA), a multivariate analysis approach particularly suitable for traits data, revealed that traits composition of infaunal and epifaunal assemblages did not vary markedly between habitats. This result was generally observed for all 10 of the infaunal, and 12 of the epifaunal, traits examined. Moreover, the proportional compositions of the various biological traits showed a high amount of within-habitat variability, even in the absence of moderate or high fishing pressure.

FCA was then used to allow an assessment of how biological trait compositions were related to total fishing pressure, both within and between habitats. The results suggested that the effects of fishing on trait compositions are complex; assemblages vary in their response both within and between habitats and, while some biological traits showed more-or-less consistent responses across habitats, others displayed varying relationships with fishing pressure across habitats. There is evidence to suggest that at least some of this habitat-specificity in response reflects differences in fishing gear, as opposed to differences in the inherent responses of the biological assemblages between habitats. We discuss the implications of these findings with respect to the impacts of fishing on the functional properties of seabed biological assemblages, and how the results presented here are to be used further within other work being conducted under Benthis.

1. INTRODUCTION

Human activity has comprehensively altered marine ecosystems and will continue to do so, some workers reporting 41% of marine areas are already strongly affected by multiple anthropogenic perturbations (Halpern *et al*., 2008). Coastal and shelf seas are particularly susceptible as they host a disproportionately large fraction of productivity and, because of the economic benefits that humans accrue from living in close proximity to the coast, such regions tend to be densely populated (Gray, 1997; Hinrichsen, 2010). Ecosystem functioning and biodiversity of coastal and shelf seas are, therefore, under pressure from a multitude of threats, such as pollution, eutrophication, and habitat loss through physical modification of the seabed (GESAMP, 1990; Gray, 1997). One of the most widespread yet manageable pressures imposed on the seabed is disturbance of the substrate by towed demersal fishing gear (bottom fishing and dredging; referred to as 'fishing' hereafter) (Collie *et al*., 2000; Eastwood *et al*., 2007; Kaiser *et al*., 2002). In UK waters, for example, the footprint of fishing is reckoned to account for over 99% of the known footprint of all human pressures on the seabed (Foden *et al*., 2011), and it is likely that this statistic similarly applies to most European shelf waters (e.g. Pecceu *et al*., 2014). Demersal fishing gears are deployed on every continental shelf in the world (Collie *et al*., 2000) with nearly 20 million km^2 (75% thereof) subjected to this anthropogenic activity (Kaiser *et al*., 2002) while Kaiser *et al*. (2000, 2006) described fishing as "*one of the greatest sources of anthropogenic disturbance to marine benthic communities*". It is, therefore, essential that both the current and future management of fishing activities are based on an improved scientific rationale, if we are to improve the long-term sustainability of this activity.

Over the past forty to fifty years, many studies have been conducted specifically intended to progress our understanding of the impacts of the various bottom fishing gear on seabed communities (e.g. Bergman *et al*., 2002; Dayton *et al*., 1995; Hall, 1999; Jennings and Kaiser, 1998; Jennings *et al*., 2001; Kaiser *et al*., 2000; Queiros *et al*., 2006). A number of field approaches have been undertaken, including large-scale field studies across known fishing gradients, experimental manipulations and comparisons of benthic assemblages from fished and non-fished regions. Although observed impacts tend to be wide-ranging, depending upon the gear type, fishing intensity, spatial coverage and the nature of the seabed (Hall, 1999; Kaiser and de Groot, 2000; Smith *et al*., 2000; Tillin *et al*., 2006), these studies consistently reveal dramatic effects of bottom fishing on the structure of marine ecosystems (Collie *et al*., 2000; Kaiser *et al*., 2006). It is, however, widely acknowledged that there are certain limitations to the conclusions reached in many of these studies. This is largely due to a lack of baseline information prior to fishing, a paucity of unfished representative control sites, difficulties in differentiating the effect of fishing from the natural background variability and the practical challenges of investigating the relatively deep regions of some shelf habitats (Jennings and Kaiser 1998). While the direct and immediate (i.e. acute) impacts of trawling on benthic assemblages have been extensively studied, it has been suspected (e.g. Hinz *et al*., 2009) that conclusions from such experimental studies can-not be readily extrapolated to an ecosystem level. Indeed, subtle cumulative effects may only become apparent when fishing disturbances are examined over larger spatial and temporal scales. The fundamental argument remains not on whether fishing impacts marine habitats, but rather how large the effects are in different habitats. Fishing leads to a reduction of the number of species and species diversity and a significantly altered taxonomic assemblage structure (Engel and Kvitek, 1998; Kaiser *et al*., 1998; McConnaughey *et al*., 2000; Jennings *et al.,* 2001; Thrush and Dayton, 2002; Kaiser *et al.,* 2003). Demersal fishing results not only in the removal of both target and non-target species, but it can also alter habitat complexity; remove, damage or kill biota, thereby reducing overall benthic production; and can lead to substantial changes in benthic community composition (Dayton *et al.,* 1995; Auster and Langton, 1999; Kaiser *et al.,* 2002; Hiddink *et al*., 2006; Kaiser *et al.,* 2006). Thus, it is perhaps not surprising that the impacts of demersal fishing have been observed to be dramatic in certain areas.

It has become apparent that there is a great variability in the susceptibility of different benthic habitats to respond to a given fishing pressure (Hiddink *et al*., 2007; Kaiser *et al*., 2006) and biogenic habitats tend to show the greatest sensitivity to fishing. However, it has often been difficult to detect any fishing impact whatsoever in shallow, soft-sediment habitats, which already experience a relatively high level of natural physical disturbance. More stable, sheltered or complex habitats are therefore usually found to be more profoundly affected by fishing activity and fishing results in long-term community changes (Jennings and Kaiser, 1998). Assemblages within these regions (e.g. mud and sand sediments in deeper waters) experience fewer natural disturbances and the associated communities are often dominated by long-lived, slow-growing species, that generally take time to recolonise after a disturbance event (Kaiser and Spencer, 1996, Kaiser *et al.,* 1998, Hiddink *et al.,* 2006, Queirós *et al*., 2006). In contrast, organisms living in habitats with a relatively high degree of natural disturbances are adapted to periodic sediment resuspension and smothering (Collie *et al.,* 2000) and are less likely to undergo long-term changes in species composition in response to the disturbance caused by fishing (and other) activities (Kaiser, 1998).

One notable feature regarding most field studies is the focus on structural impacts. It is now widely appreciated (e.g. Elliot and Quintino, 2007) that observing changes in structural attributes of benthic assemblages provides only a limited capacity to inform us of the implications for ecosystem function that is at the heart of more recent EU policy drivers, such as the reform of the Common Fisheries Policy (CFP) and the Marine Strategy Framework Directive (MSFD). Recent studies show that, following both natural and anthropogenic stressors, functional impacts and functional recovery trajectories are not always matched by their structural counterparts (Cooper *et al*., 2008; Grilo *et al*., 2011; Bolam, 2012; Wan Hussin *et al*., 2012). Marine benthic habitats and their communities provide a wide range of goods (e.g. biomass, minerals, energy) and services (e.g. nutrient and carbon recycling, life support, atmospheric regulation) and changes in biological indicators, based on structural attributes, may not necessarily result in significant changes in the overall functioning of the ecosystem, or their associated provisions of goods and services. Consequently, the conservation of marine systems requires knowledge of not only the species present, but also of how the system works and the effects of multiple and potentially co-interacting threats (Bremner, 2008). To fully determine how an ecosystem is affected by anthropogenic pressures, emphasis has to be placed on its functioning (Elliott and Quintino, 2007; Duarte *et al*., 2013).

Sustaining a balance between marine resource exploitation and biodiversity so as to protect ecosystem functioning is the *raison d'être* of the ecosystem approach (CEC, 2008). It aims to safeguard function as well as biodiversity. Therefore, an ecosystem approach to fishing impacts means that benthic function needs to be understood before it can be managed. While directly measuring ecological function (e.g., food availability for higher trophic levels, nutrient flux with overlying water) remains time-consuming and methodologically and logistically difficult, the recent development of a number of numerical analytical approaches has allowed alterations to functioning to be estimated and functional recovery compared with that of structural recovery (Cooper *et al*., 2008; Barrio Froján *et al*., 2011; Wan Hussin *et al*., 2012). The relatively recent application of Biological Traits Analysis (BTA) in particular has provided an enhanced understanding of the responses of the benthic functioning resulting from a number of anthropogenic pressures (e.g. Bremner *et al*., 2003; Tillin *et al*., 2006; Papageorgiou *et al*., 2009; Frid, 2011; Wan Hussin *et al*., 2012; Oug *et al*., 2012; Munari, 2013; Borja and Elliott, 2013; Bolam *et al*., 2014) and along environmental gradients (Dimitriadis *et al*., 2012; Van Son *et al*., 2013). Utilising assemblage information to determine what the organisms do within the ecosystem (i.e., their 'traits') as opposed to merely their taxonomic identity (i.e. what they are) offers great advances into our understanding of the functional capabilities of assemblages (Bremner, 2008). Currently, little is still known about how these approaches can be useful in marine ecological assessments and management, although they have been successfully and widely applied in both freshwater and terrestrial ecosystems (Guilpart *et al*., 2012; Colas *et al*., 2014). Functional diversity, i.e., the diversity and range of functional traits possessed by the biota of an ecosystem (Wright *et al*., 2006), is likely to be the component of an ecosystem most relevant to the functioning of ecosystems (Hooper *et al*., 2004). Nonetheless, there is neither an accepted suitable method for the measurement of functional diversity, nor adequate information regarding the actual traits to be used for its derivation (Petchey and Gaston, 2006). In view of this, one accepted biological traits approach is to use information regarding the variability in the relative composition of trait categories (e.g., suspension- surface- and subsurface deposit-feeders, carnivores, scavengers) to infer some aspect of functioning. For example, an assemblage dominated by suspension-feeding individuals will transport carbon and energy between the seabed and the overlying water column differently from one dominated by sub-surface deposit feeders (Rosenberg, 1995), while assemblages dominated by individuals that recruit *via* planktonic larvae are likely to recolonize more rapidly following large-scale physical disturbance than those reliant on benthic or lecithotrophic larvae (Thrush and Whitlatch, 2001). Species with different biological traits are likely to respond differently to the effects of fishing and, as such, different assemblages are likely to display different functional responses due to fishing (Tillin *et al.,* 2006).

In this study, we firstly investigate the between-habitat variability in potential ecosystem functioning of benthic assemblages exposed to low or no fishing pressure. We do this, for infaunal and epifaunal assemblages independently, by comparing the relative trait compositions of these assemblages, using 10 and

12 traits for infauna and epifauna, respectively. Secondly, we determine the effects of fishing on various biological traits for different habitats in order to determine the habitat-specificity of fishing effects on trait composition.

One feature of the current study which has been beyond the current state-of-the-art, is the utilisation of data from across European shelf seas. The large spatial scale of the current study aims to ensure that the results, and conclusions derived based upon them, pertain to the European shelf in its entirety, as opposed to smaller-scale regions that often are the scales used by comparable approaches (e.g. Bremner *et al.*, 2006; Frid, 2011; de Juan and Demestre, 2012).

2. METHODS

Data from a number of organisations within Benthis WP3 were collated as part of this study to ensure that the analyses and results pertained to a large number of marine habitats and a range of fishing pressures. Given the principal aim of the current study, the underlying rationale for data inclusion was for stations from spatially-focussed surveys. That is, given the large-scale remit of this study, participants were requested to source data from sampling locations or surveys possessing a relatively wide spatial cover as opposed to dense data-points from localised habitats, which would have had the potential to bias the results. For time-series surveys, data from sampling in one year only (where accompanying environmental data, for example, was most comprehensive) were incorporated for the sampling station.

2.1 Biological data

This study analyses data regarding the infauna (those animals that live within the seabed sediment) and epifauna (those that live on the seabed) of the seabed. We undertake independent analyses of both the infaunal assemblages (herein defined as organisms sampled using quantitative grab and/or coring devices) and of the larger epifaunal assemblages (herein defined as organisms sampled using a trawl or dredge device). Although we refer to the data from grabs/cores here as ‘infauna’ we appreciate that they will comprise a representation of epifaunal organisms and, similarly, those acquired from trawls/dredges, termed hereafter as ‘epifauna’ data, will comprise some taxa generally regarded as infaunal. Our rationale for treating these data separately is that these two fundamentally different sampling devices effectively collect a different component of the seabed fauna and greatly vary in the spatial scales sampled (i.e., generally 0.1m^2 for infauna and generally hundreds of m^2 for epifauna).

Eight WP3 participants supplied data for the infaunal and epifaunal analysis (Tables 1 and 2), and the spatial cover represented by both sets of faunal data spanned large regions of the European continental shelf (Figures 1 and 2). The collection of these data was funded under the auspices of projects outside Benthis. The analyses were inherently limited to both relevant and readily-available data from the participants contributing to WP3 only and this is reflected in the large geographical gaps in the spatial extent of our analyses. The number of sample stations incorporated within the infaunal and epifaunal analyses was 819 and 1316, respectively, across the North Atlantic: Bay of Biscay, Celtic Sea, Irish Sea, Western and Eastern English Channel, North Sea, northern Norwegian shelf and western Baltic Sea, together with stations from Heraklion Bay (Mediterranean Sea) and the western Black Sea (see Figures 1 and 2 for infauna and epifauna respectively).

The environmental conditions prevailing across the range of stations varied widely. For example, the North Sea and Irish Sea have extremely diverse coastal regions with a great variety of habitats (fjords, estuaries, deltas, banks, beaches, sandbanks and mudflats, marshes, rocks and islands), the seabed mainly comprising of mud, sandy mud, sand and gravel, and coastal areas are greatly affected by nutrient and sediment plumes from rivers in the south (Rees *et al*., 2007). The seabed along much of the English Channel is typically more hydrodynamically active, with gravelly sediments often occurring as thin veneers overlying bedrock (Irving, 2009). In contrast, the Kattegat, together with the Danish Straits, forms the transition zone between the North Sea/Skagerrak and the Baltic Sea. Here, circulation is dominated by north-flowing surface water with a salinity gradient of 15 to 30 ‰, and south-flowing deep water with salinities between 30 to 34 ‰. The region off the northern Norwegian shelf is relatively very deep, with cold, more-or-less motionless, bottom waters overlying generally muddy seabed habitats (Dolan *et al*., 2009). The Black Sea is a marine habitat of low salinity around 16 to 18 ‰ with an average water temperature of 11 °C, characterized by a hypoxic zone below depths of 150 m (Zaitsev and Mamaev, 1997; Sorokin, 2002). The southern-middle Black Sea Shelf (the case study area) is relatively wider in distance from land than the eastern and western Black Sea coastal shelves. The region is a shallow marine habitat with soft bottom sediment (sandy mud, muddy sand) with limited hard bottom as local patches. The Heraklion Bay sampling area in the Aegean Sea, is characterised by relatively high salinity and high bottom water temperatures, and covers both biogenic sediments and shelf muds (Smith *et al*., 2000).

In this study, it was important to maximise the comparability of the data in order to minimise observations made being the result of differences between data sources. Trait composition is not significantly affected by differences in the area of sediment surface sampled (i.e. between $0.1m^2$ and $0.25m^2$) by various grabs and/or corers (WP3 unpubl. data; 2013). Additionally, in view of the large spatial extent of our data sources, we considered it acceptable to include data derived from samples taken over a range of years, although steps were made to ensure that data from a comparable season (spring, early summer) were selected. Although the infaunal data from HCMR (Greece) were derived following sieving on a 0.5 mm mesh (as opposed to 1 mm), it was decided to retain them within the analysis, as studies have indicated that Mediterranean invertebrate species grow to a smaller maximum size relative to those in other European waters (Zenetos *et al*., 2002; Sonin *et al*., 2007). Similarly, there was little consistency in the mesh size used during sampling and/or subsequent processing of trawl samples across the various sources (Table 2) and we accepted the range of 4 mm (Norway) to 22 mm (Belgium). Finally, as stations varied in the number of replicates sampled, data from a single replicate from each station were selected, because we were interested in elucidating broad-scale spatial patterns rather than temporal trends.

Table 1. Summary of source data used for the infaunal analysis.

Participant	Region	No. stations	Year	Sampling device	Mesh (mm)
Bangor	Irish Sea	23	2007	Day grab, Box corer	1
Cefas	North Sea, English Channel	511	2000-09	NIOZ corer, mini-Hamon and Day grab	1
CFRI/OMU	Middle Black Sea	18	2013	van Veen grab	1
DTU_Aqua/DCE	Kattegat	22	2006	Haps corer	1
HCMR	Heraklion Bay, Aegean Sea	7	1995-96	Smith-McIntyre grab	0.5
ILVO	Belgian part of North Sea	59	2004-08	van Veen grab	1
IMARES	Southern North Sea	100	1995-2010	NIOZ corer	1
IMR	Northwest Norwegian shelf	79	2006-11	van Veen grab, Box corer	1
	Total stations	**819**			

Table 2. Summary of source data used for the epifaunal analysis.

Participant	Region	No. stations	Year	Sampling device	Mesh (mm)
Bangor	Irish Sea	21	2007	2m beam trawl	5
Cefas	North Sea, English Channel	496	2000-09	2m beam trawl	5
CFRI/OMU	Western Black Sea	16	2010-11	Bottom trawl	20
HCMR	Heraklion Bay, Aegean Sea	6	1995-96	2m Agassiz trawl	10
ILVO	Belgian part of North Sea	45	2004-08	8m beam trawl	22
IMARES	Dutch shelf	531	1995-2010	Dredge	5
IMR	Northwest Norwegian shelf	133	2006-11	Beam trawl	4
IFREMER	Celtic Sea, Biscay	68	2012-13	Otter trawl	20
	Total stations	**1316**			

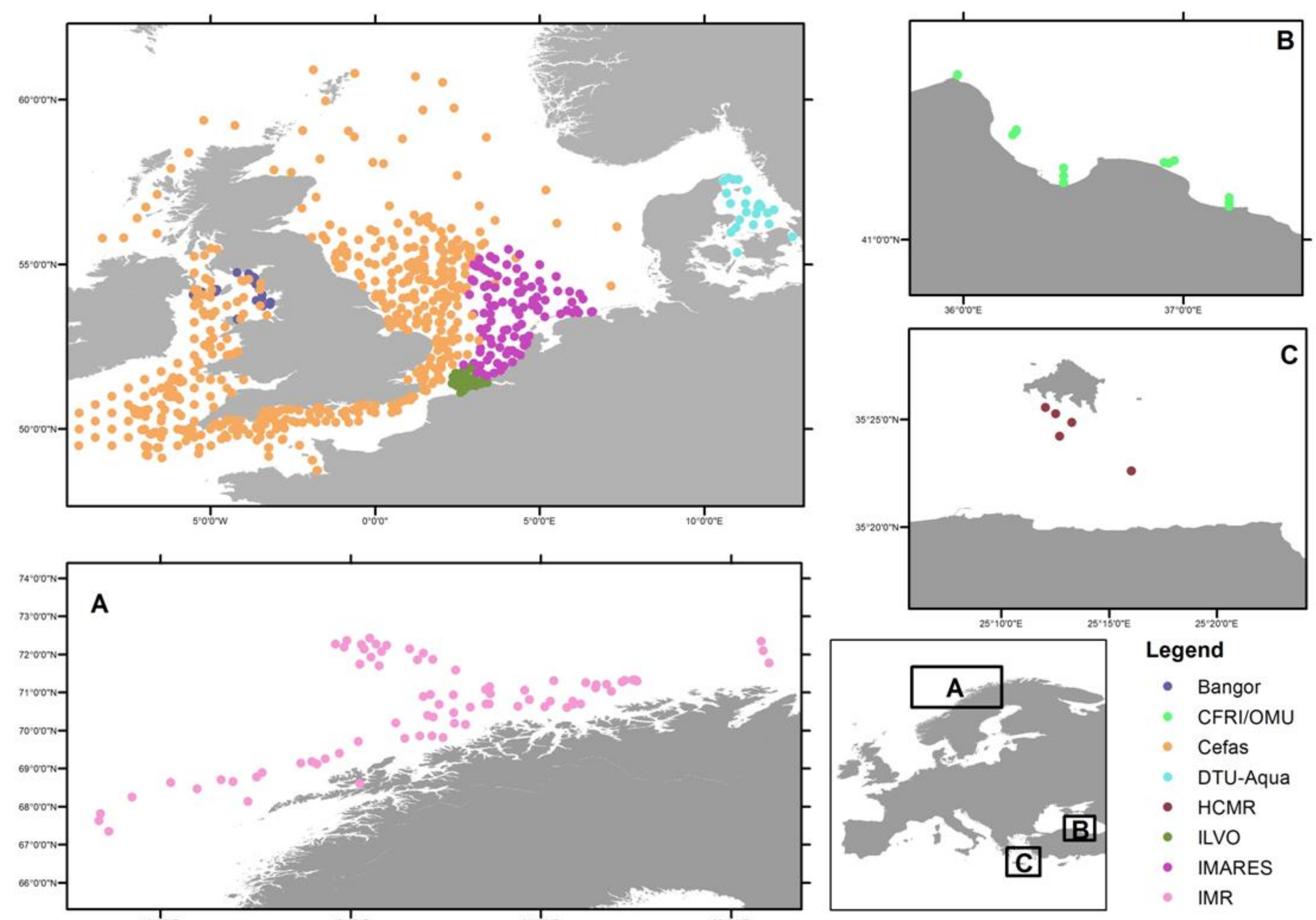


Figure 1. Distribution of the 819 stations included in the infaunal analysis. Stations are coloured according to the source participant within WP3. Note, scale varies between the various insets.

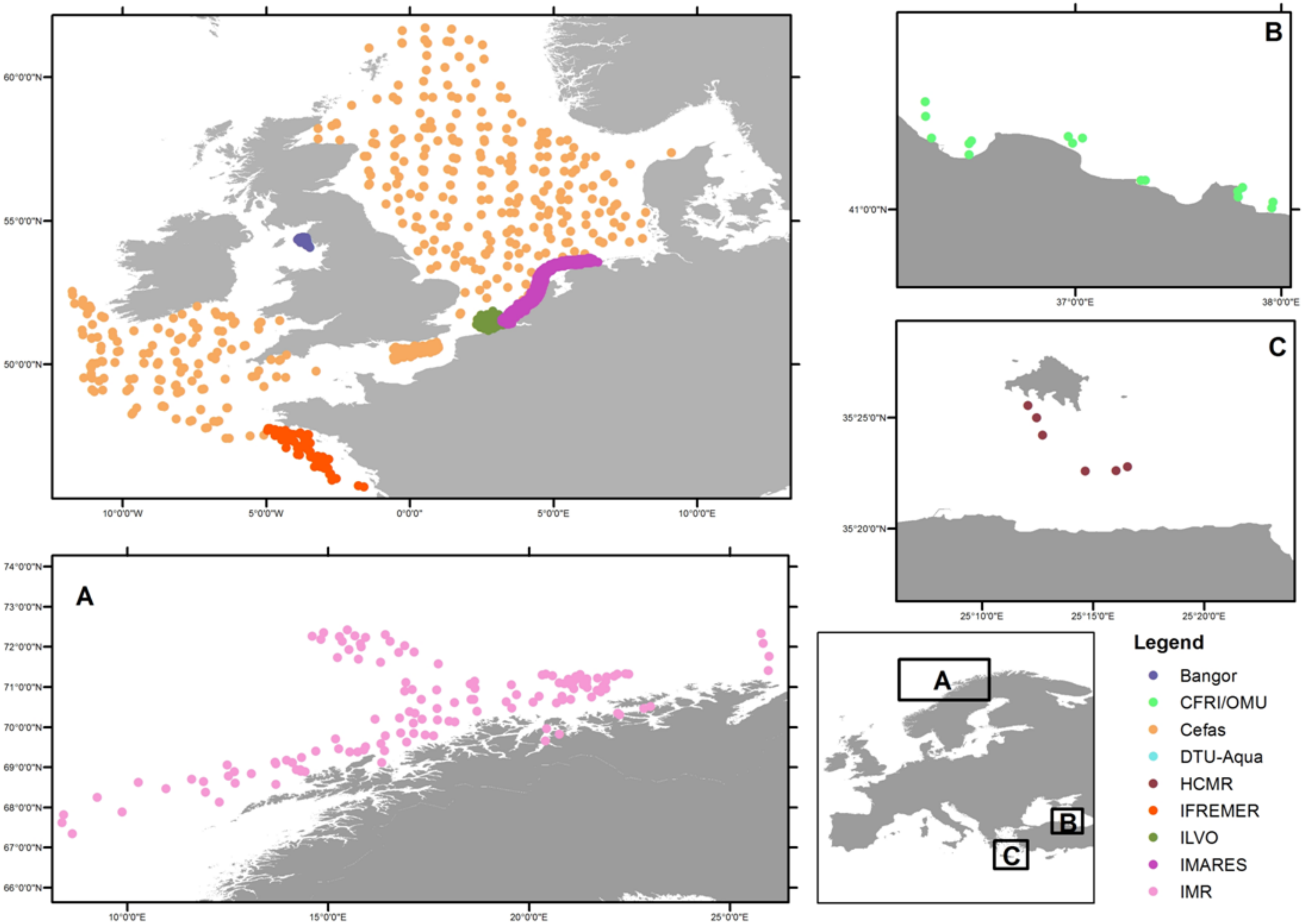


Figure 2. Distribution of the 1316 stations included in the epifaunal analysis. Stations are coloured according to the source participant within WP3. Note, scale varies between the various insets.

2.2 Biological traits

A suite of 10 and 12 biological traits were considered most relevant to describe important functional attributes of the infaunal and epifaunal assemblages, respectively (Table 3). There is currently no accepted methodology for selecting the most appropriate traits for a given study (Marchini *et al*., 2008; Bolam, 2013) and often the final selection is partly guided by the limited biological information available for benthic invertebrate taxa (Bremner, 2008; Marchini *et al*., 2008; Tyler *et al*., 2012; Munari, 2013; Bolam and Eggleton, 2014). Since traits were used in this study as a proxy for assemblage function, an attempt to focus on 'functional effects' traits as opposed to 'response' traits was made. Functional effects traits are those which affect ecosystem properties, while response traits are those which affect a species' response from changes in the environment, such as disturbance (Lavorel and Garnier, 2002; Hooper *et al*., 2004). While focussing on effects traits may seem logical for this study, there is currently a limited understanding of which traits may be regarded as functional effects traits or have direct relevance to a particular ecological function (Hewitt *et al*., 2008; Pakeman, 2011). Processes of importance in marine ecosystems are nutrient fluxes across the sediment-water interface, bioturbation and irrigation, habitat creation, secondary production, sediment stability/transport and carbon sequestration (Hewitt *et al*., 2008). Thus, each of the 10 and 12 traits for the infauna and epifauna in our final selection, we believe, are either directly linked to these processes or are indirect indicators of these processes (as per Lavorel and Garnier, 2002). The two additional traits for epifauna (i.e., 'protection' and 'habitat modification'; Table 3) were decided to be of relevance to epifaunal organisms, but less so for the infauna. The traits analysis undertaken in this study focussed on assessing the variability in trait composition of each assemblage of each habitat type and in response to fishing pressure, using each trait in isolation, as opposed to combinations of traits or all traits together (see section 2.6). As such, *a posteriori* assessments of the variability of the various trait combinations for particular functions can be performed.

Each of the traits was subdivided into multiple 'categories' chosen to encompass the range of possible attributes of all the taxa; for example, categories for the trait 'mobility' were swimming, burrowing, crawling or sessile (Table 3). A total of 47 and 53 categories represent the traits for infauna and epifauna respectively (Table 3). Some of the traits referred to measurable characteristics (e.g. maximum size, longevity) whose categories presented a quantitative scale (Paganelli *et al*., 2012) whereas others (e.g. mobility) were wholly qualitative characteristics whose categories represented discrete classes. It was considered necessary to vary the 'morphology' trait categories between infaunal and epifaunal organisms to suitably accommodate the types of organisms within each of these two ecological components.

It would be wrong to assign most taxa unequivocally to a single trait category, because many taxa display multi-faceted behaviour depending upon, for example, the specific conditions and resources available (Usseglio-Polatera *et al*., 2000). Therefore, we adopted a "fuzzy-coding" approach (Chevenet *et al*., 1994), assigning a score between 0 and 3 to each category, depending on the affinity of that taxon for that category; where 0 conveys no affinity, 1 or 2 express partial affinity and 3 indicates total and exclusive affinity. In reality, specific traits such as maximum size, longevity, and larval and egg development were predominantly expressed as partial categories for most taxa while, in contrast, entries for other traits were often represented by a total affinity for one particular category.

Information regarding all biological traits for all taxa recorded from the matrices of 819 (infauna) and 1316 (epifauna) sampling stations was required; this was sourced mainly from published papers and books and the websites of various scientific institutions (e.g. http://marlin.ac.uk/biotic/). The combined taxon list (~ 900 and ~ 1000 for infauna and epifauna, respectively, prior to any truncation) was notably larger than reported in other BTA studies on marine benthic invertebrates (e.g. 38 (de Juan *et al*., 2007); 279 (de Juan and Demestre, 2012); 101 (Tyler-Walters *et al*., 2009); 31 (Frid, 2011)), due to the relatively large spatial scale of our study and the decision not to restrict the analysis to just the discriminating taxa. The vast majority of the biological trait information (particularly for the infauna) was sourced under the auspices of recent Cefas-led projects; this data source has been used for a number of resulting peer-reviewed publications (e.g., Bolam *et al*., 2014; Bolam and Eggleton, 2014; Bolam, 2014). Trait information for additional taxa not listed within the Cefas database was acquired by each WP3 participating organisation: a shared mastersheet was produced to help reduce duplication of effort and to assist in ensuring that trait information was as comparable as possible for any given taxa, while simultaneously allowing for the inclusion of trait variation associated with geographical differences, where relevant.

While it was possible to access reliable information for many taxa regarding certain traits (e.g. larval development mode, morphology), published information describing other traits (e.g. longevity) was not available for large proportions of the taxa. In such cases, rather than assigning a score of zero to all categories for a trait (Chevenet *et al*., 1994), we adopted the category entries for the most closely-related taxa, consistent with the Best Professional Judgement (BPJ) approach employed by other workers (e.g. Tyler-Walters *et al*., 2009). One might assume that this method was more suitable wherever the entries across closely related taxa were fairly consistent, compared to those where traits were variable across closely related taxa. For cases where the latter was observed, it was necessary to spread the fuzzy-scores across a wider number of categories.

The resulting taxon-by-trait matrix was combined with the taxon abundance-by-station (No. per m^2) matrix to create the final station-by-trait matrix on which all subsequent trait analyses were based (see Figure 3) (Marchini *et al*., 2008; Munari, 2013). This results in an abundance by trait and station matrix. This matrix is fundamentally comparable to a multivariate species abundance matrix, which forms the basis of many multivariate analysis procedures of community structure, only here each station is presented by its proportional contribution of each trait category (summed for all its constituent taxa). The decision to base the trait analyses on abundance data as opposed to biomass data in this study was constrained by data availability. That is, abundance data were available for all faunal datasets, while only a sub-set of the data had associated taxon-specific biomass data. Biomass may be regarded as a more suitable metric to assess an organism's presence with regard to functioning, as it provides a better descriptor of the amount of carbon and other ecosystem resources an organism represents (Bremner *et al*., 2006). Furthermore, Herman *et al*. (1999) found benthic biomass to be strongly correlated with a number of ecological processes (e.g., primary productivity) in estuarine systems, and bivalve size (biomass) has been observed to be closely related to ecosystem function (nutrient and oxygen exchange across the sediment–water interface) (Norkko *et al*., 2013). While we appreciate that our outcomes are likely to be dependent upon this choice of data used (Bolam and Eggleton, 2014), we must appreciate the implications of this logistical constraint when interpreting the ecological significance of our results.

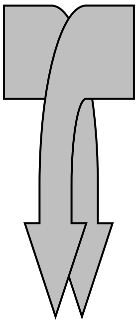
Species abundance matrix

	Stn 1	Stn 2	Stn 3
Species a	22	1	2
Species b	4	88	50
Species c	0	13	134

Taxon by trait matrix

	Trait 1			Trait 2		Trait 3		
	Cat1	Cat2	Cat3	Cat1	Cat2	Cat1	Cat2	Cat3
Species a	0.5	0.5	0	0.75	0.25	0.25	0.25	0.5
Species b	0.33	0.33	0.33	1	0	0	0	1
Species c	1	0	0	0.33	0.66	0.66	0	0.33

Summed for all taxa



Station by trait matrix

		Stn 1	Stn 2	Stn 3
Trait 1	Cat1	12.3	42.5	151.5
	Cat2	12.3	29.5	17.5
	Cat3	1.3	29.0	16.5
Trait 2	Cat1	20.5	93.0	95.7
	Cat2	5.5	8.8	88.9
Trait 3	Cat1	5.5	8.8	88.9
	Cat2	5.5	0.25	0.5
	Cat3	15	92.8	95.2

Figure 3. Illustration of the derivation of a station-by-trait matrix from species abundance and taxon by trait matrices. Hypothetical example based on three species and three traits having either two or three trait categories.

Table 3. Traits and trait categories used during BTA. Where differences were adopted between infauna and epifauna, these are indicated in the third column. The abbreviation for each trait category as used for presentation within FCA plots and tables (see results) is given in brackets.

Trait	**Categories (infauna and epifauna)**	**Epifaunal categories (where different from infauna)**	**Trait Definition and functional significance**
Size range (mm)	≤ 10 (s10) 11 – 20 (s11-20) 21 – 100 (s21-100) 101 – 200 (s101-200) 200-500 (s200-500) >500 (s500)		Maximum recorded size of adult (as individuals or colonies). Implications for the movement of organic matter within the benthic system as large organisms hold organic matter (low turnover) within the system relative to small-bodied species (high turnover) (Pearson and Rosenberg, 1978).
Morphology	Soft (mSoft) Tunic (mTunic) Exoskeleton (mExo) Crustose (mCrus) Cushion (mCush) Stalked (mStal)	Round-bodied (mRound) Flat/encrusting (mFlat) Stalked/pen-shaped (mPen) Stalked/fan-shaped (mFan) Stalked/complex (mComp)	External characteristics of the taxon. For the infauna, mSoft are represented mainly by annelid worms, mTunic by tunicates, mExo represents chitinous (lower crustaceans) and calcareous-shelled (e.g. bivalve and gastropod molluscs, echinoderms, higher crustaceans). Crustose, cushion and stalked traits are shown by various sponges, hydroids and bryozoans. For epifaunal traits, mRound is represented by all taxa not showing the other trait categories and is represented by a wide range of non-colonial taxa such as crustaceans, molluscs, annelids and echinoderms.
Longevity (years)	<1 (l1) 1 – 2 (l1to2) 3 – 10 (l3to10) >10 (l10)		Maximum reported life span of the adult stage. Indicates the relative investment of energy in somatic rather than reproductive growth and the relative age of sexual maturity, i.e. a proxy for relative r- and k- strategy (Pearson and Rosenberg, 1978). Short-lived taxa (l1) include ostracods and small amphipods, while the molluscs *Buccinum* and *Arctica* represent some of the long-lived taxa.
Larval development strategy	Planktotrophic (ldPk) Lecithotrophic (ldLc) Direct (ldD)		Indicates the potential for dispersal of the larval stage prior to settlement from direct (no larval stage, e.g. cumaceans, tanaids), lecithotrophic (larvae with yolk sac, pelagic for short periods, e.g. terebellid worms) to planktotrophic (larvae feed and grow in water column, generally pelagic for several weeks, e.g. sponges, cnidarians). Affects ability to recover from disturbance with planktonic recruitment affording potentially faster recolonisation than lecithotrophic and direct development (Thrush and Whitlatch, 2001).
Egg development location	Asexual/fragmentation (edAsex) Eggs – pelagic (edSex_pel) Eggs – benthic (edSex_ben) Eggs – brooded (edSex_br)		Indicates dispersal via the egg stage and the potential susceptibility of eggs to damage from fishing. Benthic eggs (e.g., some eunicid worms) are generally more concentrated over smaller areas than eggs released into the pelagia (e.g., hesionid worms). Asexual reproduction allows the potential to increase numbers rapidly, particularly following disturbance. Brooding is widespread within the lower crustaceans (e.g., amphipods).

Living habit	Tube-dwelling (lhTube) Burrow-dwelling (lhBurrow) Free living (lhFree) Crevice/under stone (lhCrev) Epi/endo zoic/phytic (lhEpi) Attached to bed (lhAtt)		Indicates potential for the adult stage to evade, or to be exposed to, physical disturbance.). Various lhTube (e.g., serpulid worms), lhBurrow (some bivalve molluscs), lhCrevice (such as piddocks), lhFree (e.g. eumalacostracan crustaceans), lhEpi (e.g., bryozoans) and lhAtt (e.g., ascidians, bryozoans) taxa will vary in their acute reponses to trawling depending on this trait (in combination with those of other traits such as mobility and sediment position).
Sediment position	Surface (spSurf) 0 – 5 cm (spInf_0to5) 5 – 10 cm (spInf_6to10) >10 cm (spInf_10)		Typical living position in sediment profile. Organisms occupying surficial (e.g. mytilid molluscs, sponges) or shallow positions in the sediment (some bivalves) are more likely to contact trawl gear than those living deeper (e.g. some worms). Sediment position also has implications for the effect of the organism to affect sediment-water nutrient and/or oxygen exchange.
Feeding mode	Suspension (fSusp) Surface deposit (fSurf) Subsurface deposit (fSub) Scavenger (fScav) Predator (fPred)		Feeding mode has important implications for the potential for transfer of carbon between the sediment and water and within the sediment matrix. Feeding mode also has important repercussions for many biogeochemical processes (Rosenberg, 1995).
Mobility	Sessile (mobSess) Swim (mobSwim) Burrow (mobBur) Crawl (mobCrawl)		Adults of faster moving species are more likely to evade capture by trawl gear than slow-moving or sessile individuals. Mobility also affects the ability for adult recolonisation of disturbed areas.
Bioturbation	Diffusive mixer (bDiff) Surface deposition (bSurf) Upward conveyor (bUpward) Downw. conv.(bDownward) None (bNone)		Describes the ability of the organism to rework the sediments. Can either be upward (e.g. maldanid worms), downward (e.g. oweniid worms), onto the sediment (many suspension-feeders) or mixing of the sedimentary matrix (e.g. glyceriid worms). Bioturbation mode has important implications for sediment-water exchange and sediment biogeochemical properties.
Protection		Fragile (pFrag) Unprotected (pUnprot) Protected (skin/exoskeleton) (pExo) Protect (robust shell) (pRob)	Describes the capacity to withstand physical disturbance and thus the potential for the adult population to remain viable following acute fishing. Examples include; pFrag (*Atrina* sp.); pUnprot (*Capitella* sp.*)*; pExo (*Bathyporeia* sp.*, Cancer* sp.*)*; and pRob (*Arctica* sp.).
Bed/reef formers		None (brNone) Reef-builder (brReef)	Important for affecting a number of ecological properties such as biodiversity, productivity and sediment stability. Reef-builders (e.g. *Sabellaria* sp.) create an elevated structure on the seabed through chemical precipitation or concretions while bed-

		Bed-former (brBed)	formers (e.g., mussels) form dense aggregations that visually dominate the seabed

2.3 Environmental data

Environmental data were acquired for each faunal station, so as to allow an assessment of the strength of the relationship between invertebrate traits, composition and environment, under relatively non-fished situations. These data were used to derive physical environment-based habitat groups (see Section 2.4). Environmental data needed to be comparably derived across all participants as much as possible. The following environmental parameters could be acquired for all infaunal stations:

- Depth;
- % gravel, sand, silt/clay;
- Mean annual bed temperature;
- Mean bed flow;
- Maximum (wave) peak bed flow.

The available environmental data for the epifaunal stations was somewhat more limited. Bed temperature and bed flow data were not available for a great proportion of stations and sediment granulometric data were generally not obtained for trawl samples. As such, only depth information was available for all epifaunal stations. This limited the analysis of the relationships between epifaunal trait composition and environmental variables, with implications for the investigation of relationships with EUNIS and k-mean clustering habitats (see later).

2.3.1 Depth

Depth was determined from a digital elevation model of the UK continental shelf (Astrium Oceanwise, 2011), or, for data from some sources, from measured depths taken from survey logbooks.

2.3.2 Sediment particle size

The resolution of sediment granulometric data varied between participants, ranging from full granulometric data (full phi composition) to just silt/clay (mud), sand and gravel compositions. Therefore, sediment particle size data were aggregated to the latter three sediment size class groups as % total by weight, for all infaunal stations. Particle size data were only available for a small number of epifaunal stations.

2.3.3 Mean annual bed temperature

For stations located within the UK continental shelf and within the North Sea (i.e., data from Cefas, Bangor, IMARES and ILVO), mean annual bottom temperature (2000-07) was derived from a 10 km gridded model based on ICES observations (Berx and Hughes, 2009). Other participants supplied bottom temperature estimates from regional models or published literature. Temperature data for the stations in the Mediterranean Sea were derived from modelled data from the HCMR Poseidon meteorological forecasting model (http://www.poseidon.hcmr.gr). Mean bed temperature data was not available for a number of epifaunal stations.

2.3.4 Bed flow

Wave and currents were modelled on the European continental shelf in the region between 48° N and 58.5° N and 10° W to 10° E, with a grid resolution of approximately 11 km (1/6 degree east-west, 1/9 of a degree north-south). Depth mean tidal and wind driven currents were calculated using the POLCOMS model (Holt and James, 2001) forced with 15 tidal constituents (Q1, O1, P1, S1, K1, 2N2, μ2, N2, ν2, M2, L2, T2, S2, K2, M4) and hourly wind and pressure at 12 km resolution from the UK meteorological office mesoscale atmospheric model. The meteorological forcing used was for the year 2000. Using the same meteorological forcing, the WAM spectral wave model (Osuna and Wolf, 2004) was used to provide the root mean square (RMS) wave orbital velocity at the bed. Both current and wave information were sampled at hourly intervals for subsequent calculations. Validation consisted of a comparison with observed tidal constituent data for tidal heights and currents covering a representative geographical spread. Time series of seabed wave parameters have been compared with seabed lander data at two locations and surface wave heights compared with buoy data at a representative spread of stations covering the model domain.

The annual mean and peak current at 1m above bed, together with the peak near-bed wave orbital velocity, was then calculated at each observation position. Strictly, the wave velocity is that just above the wave boundary layer (typical thickness ~1 – 5 cm above the bed). Because the sea state consists of a set of superimposed waves of varying amplitude and wavelength, the issue arises of how to define a representative bed orbital velocity. For these calculations, this is taken as orbital velocity of the equivalent monochromatic wave (the single frequency wave with the same energy density as the wave spectrum), which is related to the modelled RMS wave orbital velocity at the bed. Where no bed information was provided at a station, an existing map of broad scale bed types and grain size was used to provide this information. Where a sample station with no bed information fell outside this map, a default assumption of 0.3 mm grain diameter sand was used. Sand beds were assumed to be covered with small scale ripples and the roughness was calculated by adding $\eta/7$ to z_0 where η is the ripple height (Soulsby, 1997). Although ripple heights will vary dynamically depending on wave and current conditions, a simple approach was followed by assuming a nominal constant ripple height = 2 cm. Also, for simplicity, no account was taken of wave current interaction influencing the apparent bed roughness, although this is known to be an important effect (Fredsøe *et al*., 1999).

Bottom water flows for the stations in the Mediterranean Sea were derived from modelled data from the HCMR Poseidon meteorological forecasting model (http://www.poseidon.hcmr.gr) and data for the infaunal stations in the Black Sea were derived from published sources.

2.4 Habitat classification

Central to the aims of the current study was the ability to partition the stations according to environmentally-based units or habitat types. There are a number of ways of undertaking this, while Kaiser *et al*. (2003) suggests that, when assessing the impacts of fishing, habitats should not be classified by the sediment type alone and that depth, physical and oceanographic features and species composition should be considered during habitat type definition.

Stations in this study were grouped into habitats using two different approaches: a EUNIS habitat and a k-means clustering approach. By undertaking two alternative methods of habitat classification, we aimed to assess how our understanding of trait composition variation, and the effects of fishing pressure on trait composition, is ultimately governed by the choice of methodology for habitat categorization. The paucity of accompanying environmental data for the epifaunal stations, in particular, the sediment granulometric data which would have allowed EUNIS habitat classification derivation for stations beyond the remit of EUSeaMap (see below), limited habitat classifications for these stations.

2.4.1 EUNIS habitat

All infaunal and epifaunal stations were assigned to a EUNIS habitat class (Davies *et al*., 2004). The EUNIS habitat classification aims to provide a common European reference set of habitat types, within a hierarchical classification to allow the reporting of habitat data in a comparable manner. Although the system currently has a number of constraints and drawbacks for European-wide application (see Galparsoro *et al*., 2012) its importance is demonstrated by its inclusion within a number of European policies (e.g., the Habitats Directive, the Marine Strategy Framework, the Marine Spatial Planning roadmap) as a means ensuring a common shared path and technical terminology between Member States.

The EUNIS habitat (level 4) was determined for the majority of the infaunal stations using data from EUSeaMap (Cameron and Askew, 2011). However, as actual particle size data were available for all infaunal stations, the EUNIS habitat as predicted by EUSeaMap was revised to a EUNIS class that was in agreement with the sediment type based on that derived by the grab sample. Habitat classes were modified in this way for 39% of the infaunal stations within the EUSeaMap region. For stations located outside the remit of EUSeaMap (e.g., the Mediterranean, Black Sea, Norwegian shelf), stations were classified according to their most appropriate EUNIS habitats, based on the known depth, bottom current and sediment type. It is important to note, therefore, that results based on the EUNIS habitat classification in this study (see results) were based on analyses in which many of the stations belong to EUNIS habitats differing from those predicted by EUSeaMap. The resulting number of infaunal stations for each EUNIS class resulting from this classification is shown in Table 4. For the traits analysis, we imposed an arbitrary cut-off to exclude those habitats represented by fewer than 10 sampling stations, on the assumption that so few stations cannot adequately estimate the trait composition of a habitat.

*Table 4. Number of infaunal stations allocated to EUNIS habitats for the infaunal analysis. EUNIS habitat for each station was based on observed particle size distribution and differs from that depicted by EUSeaMap for 39% of stations. * indicates habitats not included in EUNIS-based analyses due to insufficient number of stations.*

EUNIS combined description	**EUNIS code**	**No. stations**
Infralittoral coarse sediment	A5.13	24
Circalittoral coarse sediment	A5.14	86
Deep circalittoral coarse sediment	A5.15	49
Infralittoral fine sand	A5.23	90
Infralittoral muddy sand	A5.24	14
Circalittoral fine sand	A5.25	168
Circalittoral muddy sand	A5.26	59
Deep circalittoral sand	A5.27	181
*Infralittoral sandy mud	A5.33	4
Circalittoral sandy mud	A5.35	11
Deep circalittoral mud	A5.37	67
Infralittoral mixed sediments	A5.43	11
Circalittoral mixed sediments	A5.44	24
Deep circalittoral mixed sediments	A5.45	24
*Mediterranean communities of shelf-edge detritic bottoms	A5.47	4
*Maerl beds	A5.51	3

It was necessary to allocate the epifaunal stations to EUNIS levels 2 and 3 rather than the more detailed level 4, primarily due to the deficiency of accompanying particle size data. For epifaunal stations located outside the remit of EUSeaMap (Norwegian shelf, Bay of Biscay, Mediterranean Sea, Black Sea), depth and known sediment types (using sediment granulometric data if available) were used to derive EUNIS habitats to either Level 2 or 3 (depending on information available). Where this was not possible, the stations were defined as 'unclassified', albeit that this category is, in reality, likely to comprise stations from a variety of habitats. While EUNIS level 4 habitats were predicted for some stations within the spatial remit of EUSeaMap, these were assigned to the appropriate level 3 so as to aid comparability with those outside the EUSeaMap area. EUSeaMap assigned some stations as A4.2, a circalittoral rock substrate habitat, while an examination of their fauna inferred that they were sedimentary in nature. However, the absence of any other substrate data prevented us assigning such stations to any alternative habitats. The number of stations representing the various habitat classes for the epifaunal stations is presented in Table 5. As for the infaunal data, habitats represented by fewer than 10 sampled stations were excluded from numerical analyses.

*Table 5. Number of stations allocated to EUNIS habitats for the epifaunal analysis. EUNIS habitat for each station was based on predictions from EUSeaMap or using depth and sediment type information. The prefix 'U' does not represent a formal EUNIS code, but here refers to 'unclassified'. * indicates habitats not included in EUNIS-based analyses due to insufficient number of stations (< 10 in total).*

EUNIS combined description	EUNIS code	No. stations
Atlantic and Mediterranean moderate energy circalittoral rock	A4.2	42
*Atlantic and Mediterranean low energy circalittoral rock	A4.3	3
Sublittoral coarse sediment	A5.1	99
Sublittoral sand	A5.2	830
Sublittoral mud	A5.3	162
Sublittoral mixed sediments	A5.4	20
*Deep-sea mixed substrata	A6.2	2
*Deep-sea sand	A6.3	5
*Deep-sea mud	A6.5	3
Unclassified	U	83
Deep circalittoral seabed	U_DCS	53
*High energy infralittoral seabed	U_HE	1
*Low energy circalittoral seabed	U_LE	2
*Moderate energy infra- or circalittoral seabed	U_ME	4
*Upper slope seabed	U_USS	7

2.4.2 K-means cluster group habitats

A k-means clustering approach was conducted using the environmental parameters for each infaunal station (i.e., depth, sediment composition, bottom temperature, mean annual bed flow and annual peak bed flow). This approach allowed stations to be classified into habitat types based not only on a wider suite of environmental variables than that underlying the EUNIS approach, but also using variables (e.g., % silt/clay, sand, gravel) based on observed data. Furthermore, the resulting habitats were not constrained to those in character nor number to those governed by the EUNIS classification system. Due to the lack of environmental data (particularly sediment particle size), it was not possible to undertake a cluster analysis for the epifaunal stations.

The 819 infaunal stations produced 8 statistically-defined (by the Calinsky-Harabasz criterion; Calinsky and Harabasz (1974)) cluster groups with 88, 14, 7, 49, 11, 400, 46, 202 stations for Clusters 1 to 8, respectively (Table 6). The ranges displayed for each environmental metric for each cluster group are presented as box-plots in Figure 4. Depth appeared to be most influential variable defining groups, with each group displaying almost non-overlapping depth ranges. Other metrics varied with respect to their cluster differences. For example, stations in Cluster 1 exhibited notably higher gravel content relative to all other clusters, while mud content was generally high for stations within four clusters (3-5 and 7) and annual peak wave bed flows were zero for stations in Clusters 2, 3, 5 and 7. The geographical regions and environmental characteristics of each cluster group are summarised in Table 6 and Figure 5.

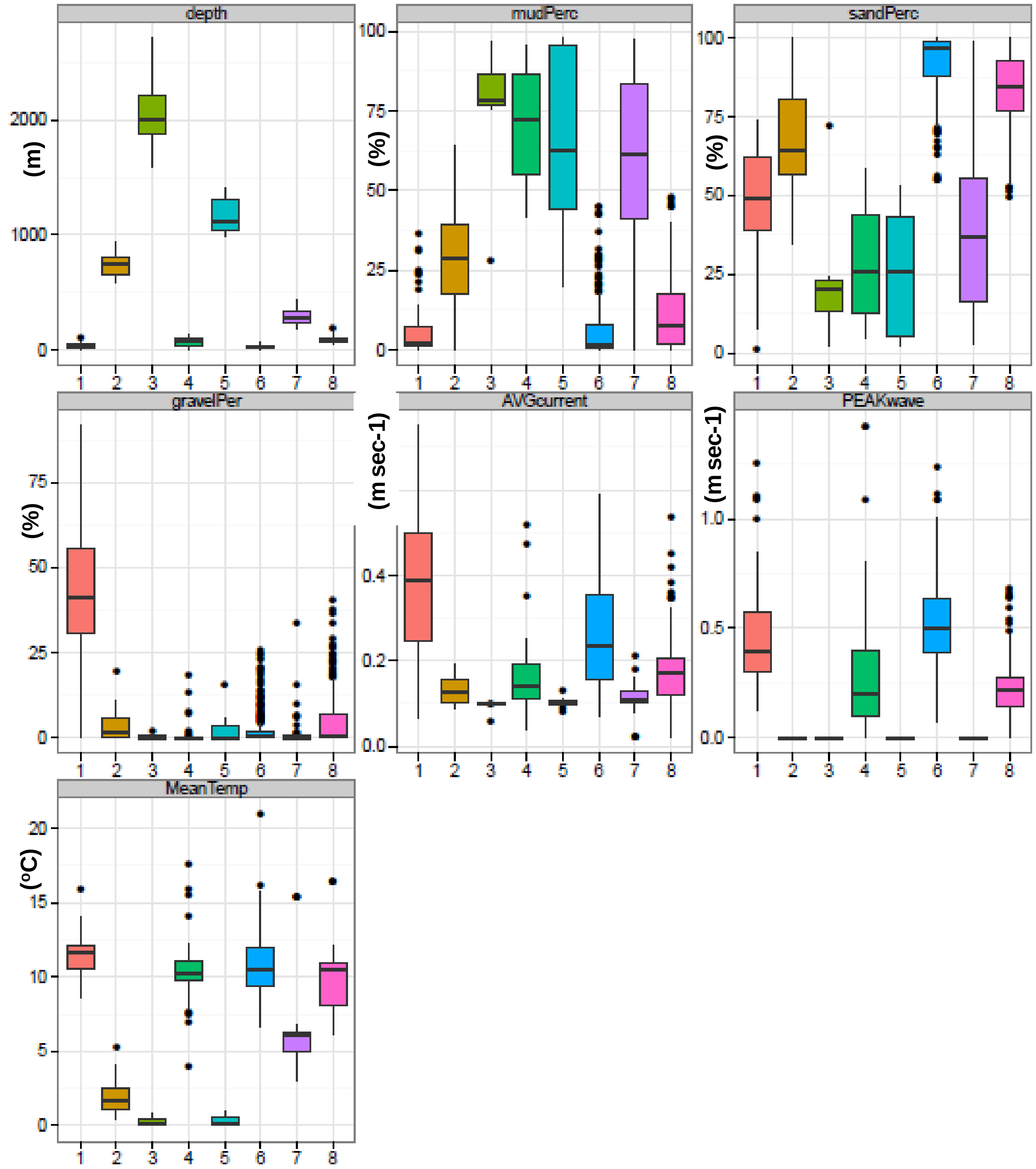


Figure 4. Box-plots showing the range of environmental variables of within Clusters 1-8.

Table 6. Summary descriptions of the environmental conditions prevailing for Clusters 1-8. Regions given in brackets are those where the cluster group represents only a very minor part of the region (i.e., is only represented by a small percentage of the stations present).

Cluster	# stations	Geographical regions	Environmental conditions
1	88	English Channel, western North Sea, Dogger Bank, Irish Sea, Black Sea	Shallow (average 40m), gravelly sand, strong bed flows with warm annual bed temp (average 11.3°C)
2	14	Norwegian Shelf	Deep (average 850m), muddy sand, low bed flows and low annual bed temperature (average 2.1°C)
3	7	Norwegian Shelf	Very deep (average 2,100m), slightly sandy mud, low bed flows and very low annual bed temperature (average 0.2°C)
4	49	Black Sea, northern Kattegat, Irish Sea, [Belgian Shelf], [North Sea],	Moderately shallow (average 70m), sandy mud with moderate bed flows and warm annual bed temperature (average 10.4°C)
5	11	Norwegian Shelf	Deep (average 1,170m), muddy to sandy mud, low annual bed flows and very low annual bed temperature (average 0.3°C)
6	400	Irish Sea, English Channel, North Sea, Kattegat, Belgian Shelf, Black Sea	Shallow (average 33m), sandy, fairly strong bed flows and warm annual bed temperature (average 10.6°C)
7	46	Heraklion Bay, Norwegian Shelf	Moderately deep (average 293m), sandy mud, low annual and peak bed flows, medium annual bed temperatures (average 6.4°C)
8	202	Western English Channel, Irish Sea, northern North Sea[Norwegian Shelf]	Medium-depth (average 93m), slightly muddy sand, medium bed-flow currents, warm annual bed temperatures (average 9.9°C)

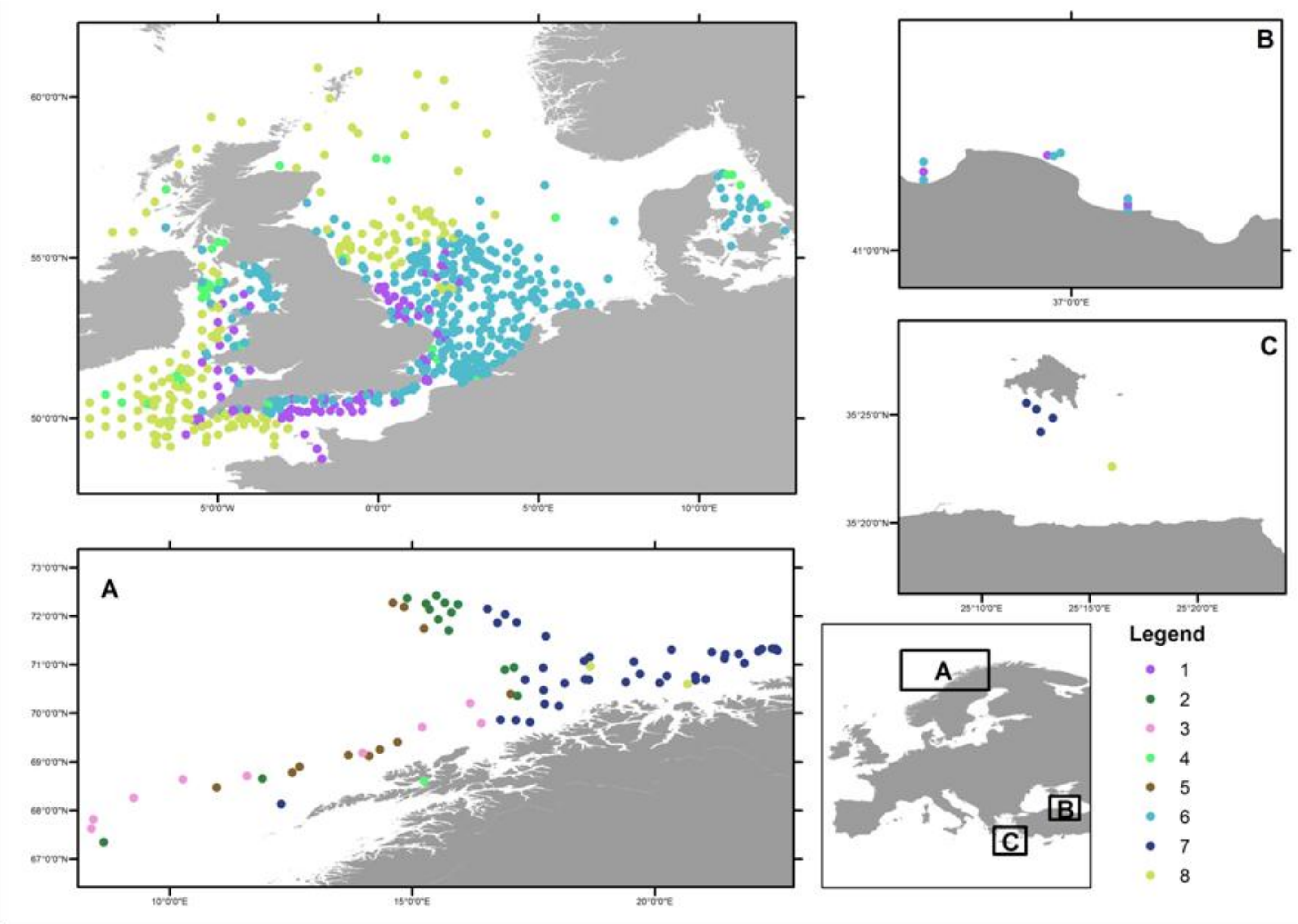


Figure 5. Distribution of the stations classed according to habitats derived by k-means clustering of environmental variables. For descriptions of the environmental characteristics of each cluster habitat refer to Table 6. Note, scale varies between the various insets.

2.5 Fishing pressure metrics

The fishing pressure metrics for the infaunal and epifaunal stations, and included in the biological traits analysis, were provided from different data sources, due to differences in data availability between case study regions and project partners:

- For the majority of the stations (those located on the Norwegian shelf; in the North Sea; the Kattegat, and in the Irish Sea) standardised BENTHIS WP2 fishing pressure estimates (yearly km^2 of swept area in grid cells of 1*1 minute longitude and latitude) were derived. All fishing activity in grid cells with their centroids less than 2 km from a given station were assumed to have had an impact, and individual swept area estimates of these cells were summed by major gear type (otter trawl, beam trawl, dredge and demersal seine) and subsequently averaged across years. This process resulted in the total FP metric values for each station that were used during the analyses undertaken in Sections 3.1 - 3.3).
- For stations in the Bay of Biscay, the FP metric values were provided by IFREMER, using a comparable approach to that described above, although it varied with respect to the method of utilising VMS data to determine vessel activity. That is, from two consecutive GPS positions (p1 and p2) the activity of the fishing vessel was defined, depending on mean speed, as; 'route' where mean speed between p1 and p2 was > 4.5 knots or where either p1 or p2 were within 2 nm of a port; 'fishing' where mean speed was ≤ 4.5 knots; or 'undetermined' where mean speed was zero or time interval between p1 and p2 was > 6 h.
- Fishing pressure for the stations within Heraklion Bay was abstracted from VMS data processed within the BENTHIS project. The data were taken from interpolated maps of fishing effort produced using the VMS tools workflow (BENTHIS Deliverable 7.6). Values used were either zero values in control stations where it has been verified that no trawling takes place, and mean values of swept area coverage from two different bandings. In addition, in one experimentally trawled area, values were calculated from the swept area trawling coverage during the trawling impact phase of the experiment.
- No fishing pressure data were available for the stations in the Black Sea. However, two groups of stations had been selected for sampling by CFRI; one group where fishing was not considered to take place (a reference area) and a heavily-fished region (impact area). While we acknowledge the lack of any quantitative data regarding fishing pressure is problematic, we assigned FP values of zero and 20 km^{-2} y^{-1} to the stations of the reference and impact areas respectively.

The BENTHIS WP2 swept area estimates used during the current traits analysis represent state-of-the-art methodology regarding the calculation of fishing pressure metrics from official catch and effort statistics. In WP2, project partners developed and applied a standardised workflow, which combined VMS and logbook data, together with estimates regarding the dimensions of the different gears (WP2, 2014). The relationships between gear dimensions and vessel size (e.g. trawl door spread and vessel engine power (kW)) for different gear groups were used to assign quantitative information of bottom contact (e.g. width of gear) to each logbook trip, and the extended logbook data were combined with interpolated vessel tracks based on VMS data (Hintzen *et al.*, 2010). The required vessel size information, in terms of engine power (kW) and vessel length overall (LOA) in metres, was collected, together with the gear specifications in an industry-based questionnaire survey. This survey was completed by 12 partners to provide a pan-European vessel and gear inventory with 1132 observations. This enabled statistical modelling of the vessel size or vessel engine power ~ gear size relationships for different métiers (combinations of gear types and target species) to be conducted.

In this way, the total seabed area (km^2) swept by a fishing gear yearly was estimated for each 1x1 minute grid cell of the BENTHIS case-study waters (1x1 minute longitude and latitude equals approx. 1.9 km^2 at 56^{o}N, this grid cell area gradually increases when moving south and gradually decreases when moving north) for a three year period from 2010 to 2012. The final workflow was completed by 14 European countries (Sweden, Germany, Denmark, England, Ireland, Belgium, The Netherlands, Scotland, Italy, Greece, Portugal, Northern Ireland, Norway) for the official statistics of VMS-equipped vessels, in order to provide high-resolution maps of fishing pressure in the Northeast Atlantic and Mediterranean waters. An example for the North Sea is given in Appendix 1, where fishing pressure intensity is split according to four major demersal gear types: otter trawls, beam trawls, dredges and demersal seines.

Not all European countries with commercial fishing fleets are BENTHIS partners, and not all partners had sufficient data access to allow completion of the workflow. Consequently, the included WP2 fishing pressure estimates do not provide full coverage of the case study areas, and this is particularly true in coastal areas, where smaller vessels below 12 meters (without VMS equipment) fish commercially with mobile, bottom contacting gears. Although the French fishing effort data were missing from the final BENTHIS WP2 dataset included in this biological traits analysis, the majority of the North Sea has significant coverage. The missing French data are, however, an issue in the southern parts of the North Sea, the English Channel, the Bay of Biscay, and in the Celtic Sea.

2.6 Numerical approaches

This study aimed to address two fundamental questions, these were:

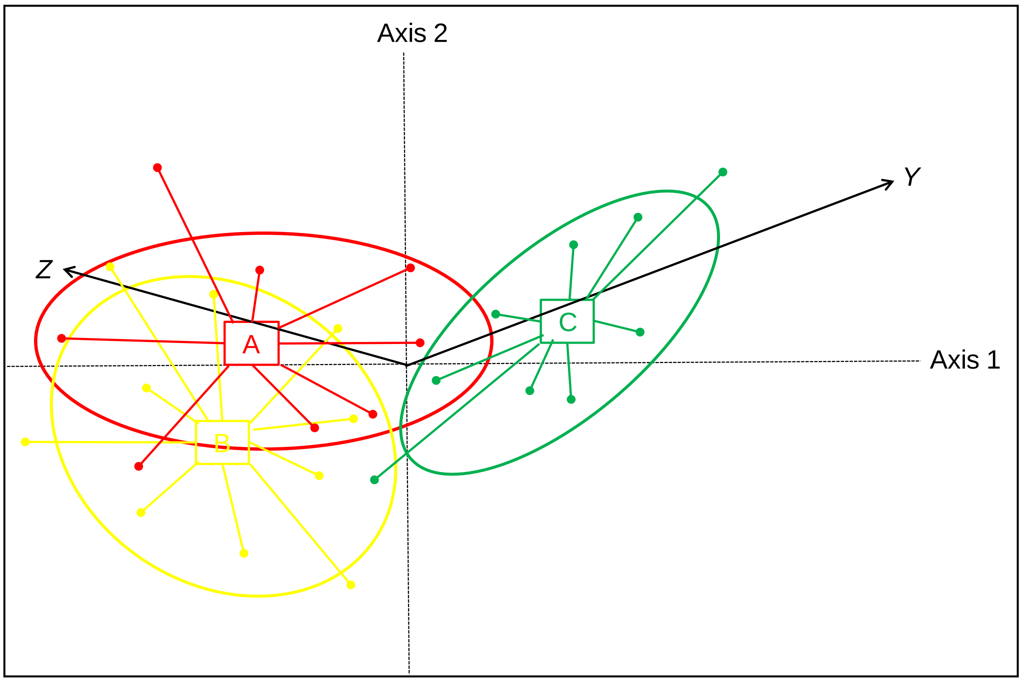
a) to what extent does biological trait composition vary between habitats under low or no-bottom fishing and, is habitat variation trait-specific?; and

b) does bottom fishing (hereafter termed ‘FP’ - fishing pressure) affect trait composition and, if so, is this trait- or habitat-dependent?

These two questions were addressed for infaunal and epifaunal assemblages separately. All trait analyses were undertaken based on each trait independently, as opposed to a single analysis in which all traits are combined (e.g. Atkinson *et al*., 2012; Fleddum *et al*., 2013). We believe that this approach allows a more straightforward appraisal of the relative differences in habitat-specificity between trait categories within each trait, as it provides an easier method by which to understand how each trait category responds, as opposed to the trait itself.

All the station by trait and station by environment data were checked for inconsistencies and gaps prior to any analyses being undertaken. To address the first aim, the distribution of FP values (EUNIS and k-means habitat classes) were analysed for each habitat separately and the stations with either no- or relatively low FP values were selected for analysis, i.e., all stations considered to possess medium or high total FP estimates for each habitat were excluded. While it would have been preferable to only include stations with zero FP estimates, this would have resulted in insufficient numbers of stations per habitat for analysis.

Based on these data, the assemblage trait compositions of each habitat were then investigated using fuzzy correspondence analysis (FCA) using the free statistical software programming package R (R Development core Team, 2006). Fuzzy Correspondence Analysis (FCA) is derived from the Correspondence Analysis (CA) ordination method, a statistical multivariate exploration method designed to analyse two-way (and, more generally, multiway) contingency tables with multidimensional qualitative or quantitative input data (Theodorou *et al*. 2007). CA uses eigenanalysis to investigate differences between samples (Legendre and Legendre, 2012). Here, we used a different version of the CA adapted to fuzzy-coded data, the FCA (Bandemer and Gottwald, 1996), in this case based on the biological traits exhibited by species present in the assemblages. It resembles a correspondence analysis and is suitable for fuzzy-coded data (Chevenet et al., 1994). FCA provides the variability contained in every axis and the correlation ratios of each biological trait along the principal axes. It also allows plotting the scores of trait category in a reduced two-dimensional factor map (also called a biplot), reducing the n-dimensional space represented by all the categories of taxa traits and, thus, summarizing the complex patterns embedded in the original dataset. Two-dimensional standardised FCA plots were produced displaying the relative trait composition of each station, categorised by habitat class. For each habitat, the mean across the two dimensional reduced space was calculated to give an average position of the “typical station” for a specific habitat, the centroid. The closer the station to the centroid, the more similar that station is to the overall characteristic of the habitat. Lines connecting the location of each station to its corresponding centroid are displayed, allowing an inspection of the variability within and between habitat centroids. Following a similar logic, the Euclidean distance between centroids in the two-dimensional space can be used to measure trait composition difference between habitats: the greater separation between centroids, the greater the dissimilarity of the trait composition between the habitats. However, one must remember that the locations of the centroids cannot encapsulate the variability in trait composition of the stations, i.e., the centroid locations are unaffected by the magnitude of the spread of the stations. Additionally, these distances must be considered with caution, since they are calculated upon two axes only, which, although integrating the majority of the inertia of the analysis, do not integrate the full extent of the inertia (i.e. it doesn’t explain the entirety of the observed pattern). Thus, in the absence of the availability of formal statistical testing for the detection of differences between habitats, the distance between centroids to infer significant difference must be used with some caution. Following an appraisal of the FCA plots alongside the values of centroid distances, it was decided that a Euclidean distance > 2 for the infaunal data and > 1.5 for the epifaunal data represented an acceptably large separations between centroids to signify a pronounced difference in trait composition between habitats. Box 1 presents an example to illustrate how differences between habitats were derived from the FCA plots in this study. Finally, as the influence of each trait category can be superimposed on the FCA plot, it is possible to determine the trait category contributing the most to any trait composition differences between habitats.



Box 1. Example of a FCA plot of the traits composition for a number of stations belonging to three habitats, A, B and C. The stations of habitat A (red dots) occupy the left portion of the plot (negative values along axis1) and show within-habitat trait differences. The median location of these stations is given by the centroids for the habitat (red box) and the spread (95%) of stations for the habitat represented by the red oval. Similarly, the locations of the stations of habitat B (yellow dots) as defined by their trait composition are also on the left part of the plot. The Euclidean distance between the centroids of habitats A and B is 0.7 (scale not shown) and this distance would signify that there is no significant difference between the trait compositions of the stations of these two habitats. The assemblages of both habitats have relatively high proportions of trait Z and relatively smaller proportions of trait Y.

The stations of habitat C are located on the right hand side of the FCA plot (positive axis1 values). As with habitats A and B there is some within-habitat variability in the proportions of the trait categories of this trait. However, there is little overlap between the stations of C with those of A and B and the Euclidean distance between A and C is 2.3 and that between B and C is 2.6. This would be interpreted as a significant difference in the trait composition of Habitat C from both that of A and B, being more numerically dominated by individuals possessing trait Y. To note, however, is that the notation of significance between C with A and B would not be affected if the within-habitat variability increased or decreased, it is based on the Euclidean distance of the centroid locations.

To address the second aim of the study, i.e. the effect of FP on trait composition, the FP estimates were used as a continuous supplementary variable during the FCA analysis. In contrast to the analysis performed to meet the first aim of the study, data from all stations were included for the second aim. A supplementary variable, unlike the "active" variable, is not used to build the analysis, it does not drive anything but is merely overlapped (or projected) afterwards to explore their pattern with respect to the ordination in reduced space drawn from the active variable. Unlike the analyses undertaken for the analyses above, separate FCA were undertaken using stations from each habitat. FCA plots reveal the positions of each station of the habitat, together with vectors for each trait category, indicating the relative influence of each trait category for the station differences. The plots also allow the inclusion of FP as a vector, because of the systematic standardisation of the FCA coordinates outputs, the euclidean length and trajectory of this vector could be used to indicate the relationship between the station positions and FP estimates. The greater the FP vector length, the greater the relationship between FP and trait composition, with the possibility for a positive relationship (vectors sharing similar trajectories) or a negative (vectors with opposing trajectories) relationship.

A Spearman rank correlation analysis was undertaken between FP and percent composition of those trait categories showing the strongest relationships with FP from the FCAs. This non-parametric correlation approach was adopted, as even log-transforming the highly-skewed FP estimates (see Section 3.1) failed to satisfy the requirements of a more sensitive, parametric correlation approach (e.g., Pearson product moment correlation). The purpose of calculating the correlations was to filter the data to pick out the pairwise comparisons for which there was evidence of linkage. We calculated p-values to do this, and considered values less than 0.05 (type I error), to be statistically significant. We considered it appropriate to set the type I error rate for each individual comparison rather than to set some overall type I error rate for all comparisons. Of course, there may well be linkage for non-statistically significant correlations – but our data was not able to demonstrate this beyond reasonable doubt.

3. RESULTS

3.1 Relationship between fishing pressure and habitat type

3.1.1 Infaunal stations

Although demersal fishing is experienced at stations across all habitats considered within the present study, FP intensity varies widely within and between habitats (Figure 6a and b). Most EUNIS habitats displayed median total FP estimates < 5 $km^{-2}y^{-1}$, although some stations experienced disproportionately high FP estimates (> 20 $km^{-2}y^{-1}$), resulting in a highly positively skewed FP distribution for most EUNIS habitats (Figure 6a). Generally, the highest FP values occur for A5.33 (infralittoral sandy mud), A5.35 (circalittoral sandy mud) and A5.37 (deep circalittoral mud), although the outlying high values tend to be found in A5.23 (infralittoral fine sand), A5.25 (circalittoral fine sand) and A5.27 (deep circalittoral sand). The highest FP values (> 75 $km^{-2}y^{-1}$) belong to three stations across differing EUNIS habitats (A5.14 - circalittoral coarse sediment, A5.25 – circalittoral fine sand, A5.35 – circalittoral sandy mud).

Fishing pressure across cluster group habitats is similarly complex and, although all cluster groups contain stations subjected to some demersal fishing, the distribution of FP both within and between cluster groups varies (Figure 6b). Stations of Cluster 4 (moderately shallow, sandy mud with moderate bed flow and relatively warm bed temperatures) are subjected to the greatest FP and this cluster displays a less-skewed FP distribution across its stations. However, a number of stations of all clusters (except Cluster 3 – very deep, slightly sandy mud, very low temperature and bottom flow) experience high fishing pressure estimates (e.g. > 20 $km^{-2}y^{-1}$).

Clearly, therefore, stations of each habitat, whether defined by EUNIS or by k-means clustering, show highly skewed FP estimates. In this respect, FP distribution is broadly comparable across the majority of habitats, with the majority of stations experiencing FP estimates < 10 $km^{-2}y^{-1}$, there are, however, some habitat differences. This habitat-specificity of FP must be borne in mind when comparing trait changes in response to fishing pressure between the various habitats. For example, variations in the trait response to FP between habitats may, in effect, actually reflect differences in FP as opposed to any perceived habitat-specific response.

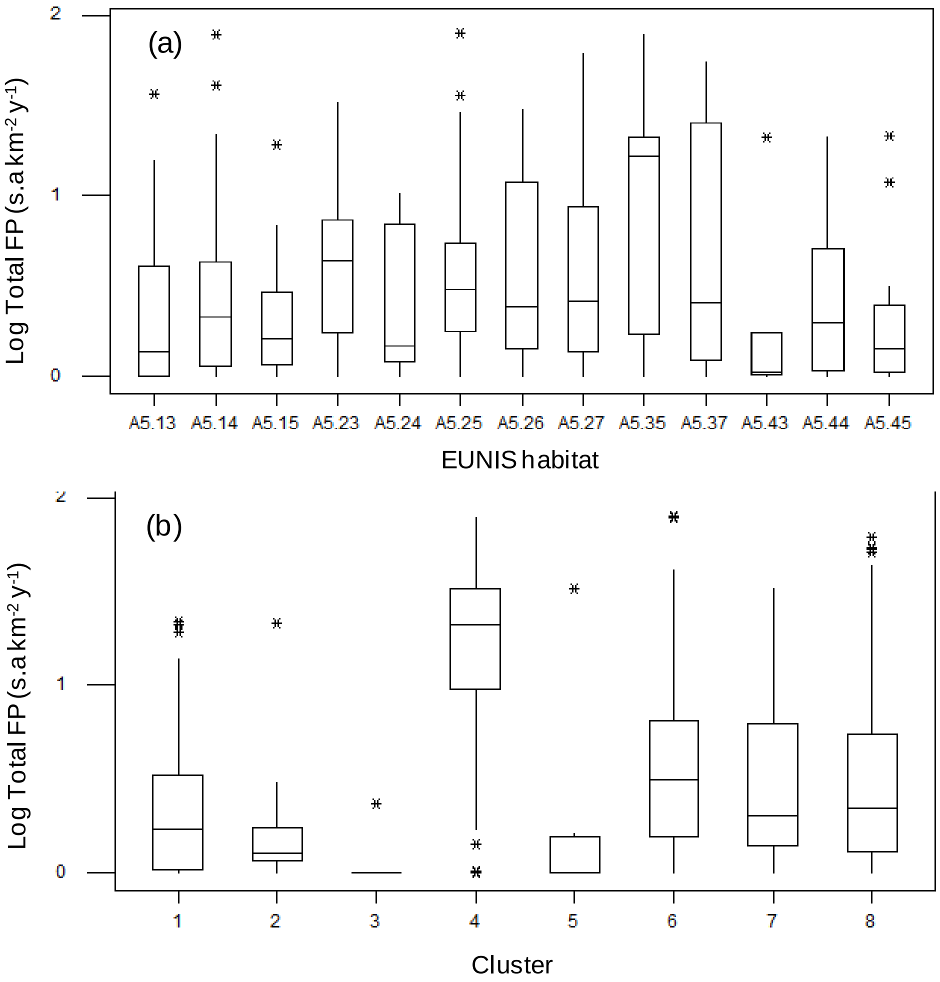


Figure 6(a and *b). Fishing pressure (swept area km^{-2} y^{-1}) for (a) EUNIS habitats and (b) k-means Cluster groups for the infaunal stations.*

There is a strong relationship between the type of fishing gear used and habitat, with total FP for most habitats being largely attributed to one type of trawl (Figure 7). While seine trawling tends to account for the majority of FP in the coarser-grained sediment habitats (A5.13 - infralittoral coarse sediment; A5.14 - circalittoral coarse sediment; A5.15 - deep circalittoral coarse sediment; A5.43 - infralittoral mixed sediment; and the shallow, relatively gravelly seabeds of Clusters 1 and 6) otter trawling principally operates in the sandier habitats and muddy sediment habitats (e.g., A5.24 - infralittoral muddy sand; A5.26 - circalittoral muddy sand; A5.27 - deep circalittoral sand; A5.37 - deep circalittoral sandy mud; and those of all habitat Clusters 2-5 and 7-8). Beam trawling did not account for the majority of fishing within any habitat, although it did account for a third to a half of total FP in a number of habitats (e.g., A5.25 - circalittoral fine sand; A5.44 - circalittoral mixed sediment).

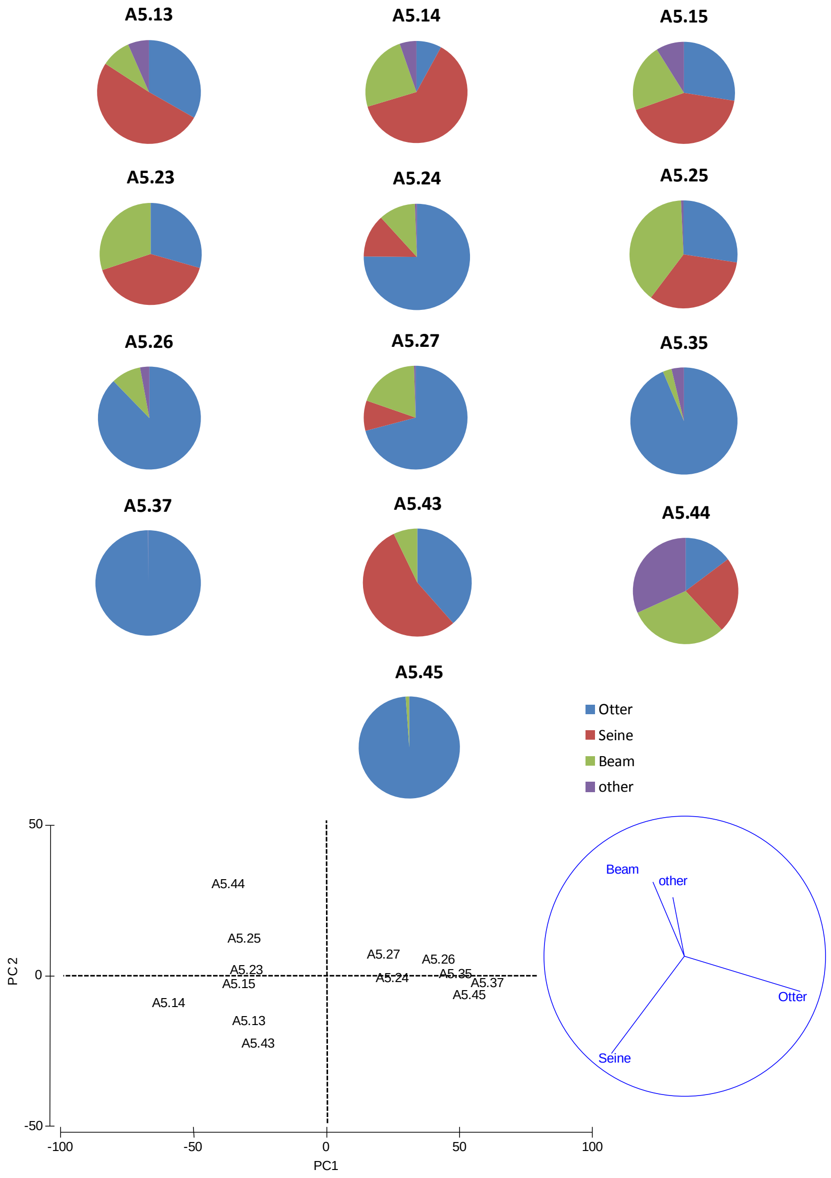


Figure 7. Relative contribution of the various gear types to total FP for infaunal sampling stations across each EUNIS habitat (top) and 2-d ordination of the relative similarity between habitats following PCA (bottom). Data for habitats for which the traits assemblages were not analysed due to insufficient numbers of stations (Table 4) are not shown. Category 'other' includes a range of gear types but principally various types of dredges.

When the stations are categorised according to habitats using a k-means clustering approach, there is less inter-habitat difference in the relative proportion of total FP by the four types of fishing gear (Figure 8). Fishing at stations of Clusters 2-5 and 7 is almost exclusively undertaken using otter trawls, those of Cluster 8 (medium depth, slightly muddy sand, warm bed temperature regions in the western English Channel, Irish Sea and northern North Sea) are also dominated by otter trawling although beam trawling supplies a notable component, while those of Clusters 1 and 6 are more targeted by seine trawling (Cluster 1 – shallow, gravelly sand with string bed flows) and seine and beam trawling (Cluster 6 – shallow, sandy regions with moderate bed flows).

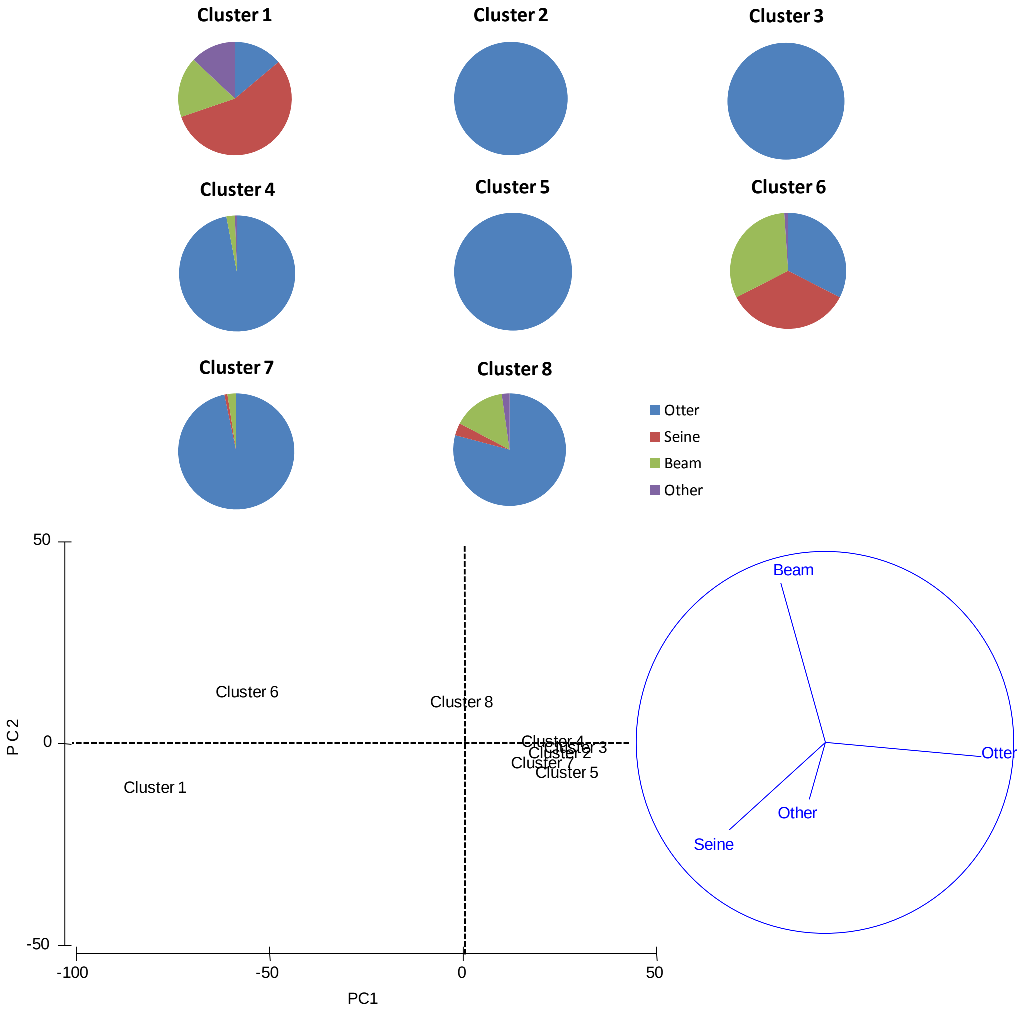


Figure 8. Relative contribution of the various gear types to total FP for infaunal sampling stations across each Cluster group habitat (top) and 2-d ordination of the relative similarity between habitats following PCA (bottom). Category 'other' includes a range of gear types but principally various types of dredges.

3.1.2 Epifaunal stations

Analogous to the situation observed for the infaunal stations, demersal fishing is undertaken across all habitats for which epifaunal data were present within our dataset (Figure 9). The only exception to this was A6.2 (deep-sea mixed substrata; not being included in analyses), the two stations within this habitat exhibiting FP estimates of zero fishing pressure. FP varies within and between habitats. The highest FP estimates were broadly observed for A4.2 (Atlantic and Mediterranean moderate energy circalittoral rock), A5.1 (Sublittoral coarse sediment), A5.3 (Sublittoral mud) and A6.5 (Deep-sea mud; excluded from analyses), although many habitats displayed positively skewed FP distributions across their associated faunal stations.

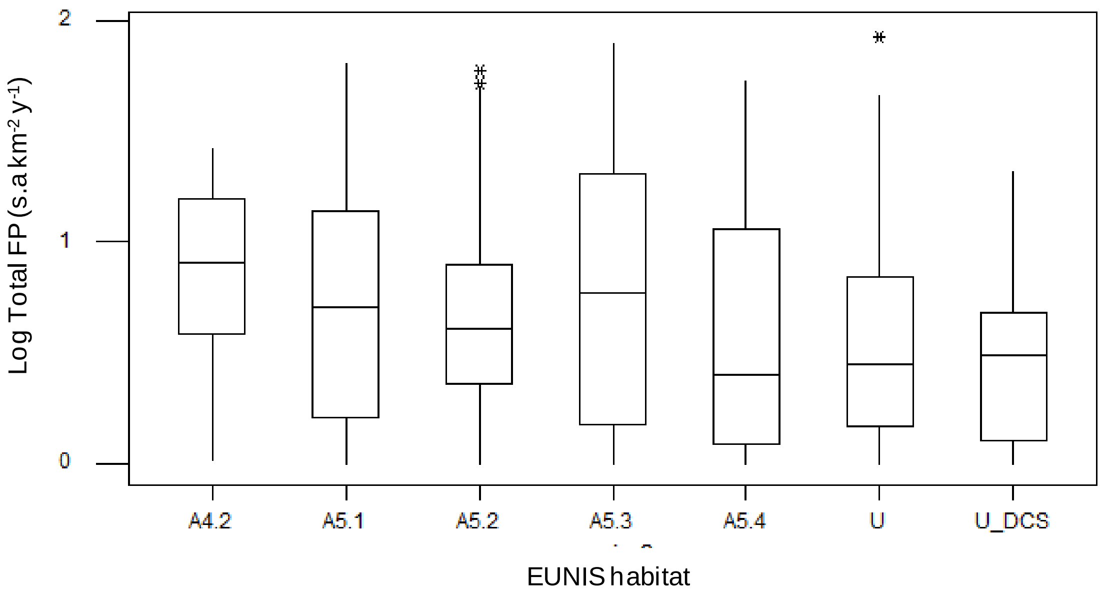


Figure 9. Fishing pressure (swept area km^{-2} y^{-1}) for EUNIS habitats for the epifaunal stations.

As was the case for the infaunal stations, there was a marked difference in the proportions of total FP across the various gear types. While seine trawling accounts for the majority of total FP in the coarser-sediment habitats (A4.2 - Atlantic and Mediterranean moderate energy circalittoral rock; A5.1 - sublittoral coarse sediment), otter trawls assume a greater proportion of total FP in A5.3 (sublittoral mud) and A5.4 (sublittoral mixed sediments) (Figure 10). Otter trawls also account for the majority of total FP in the 'unclassified' (U) and deep circalittoral seabed (U_DCS) habitats.

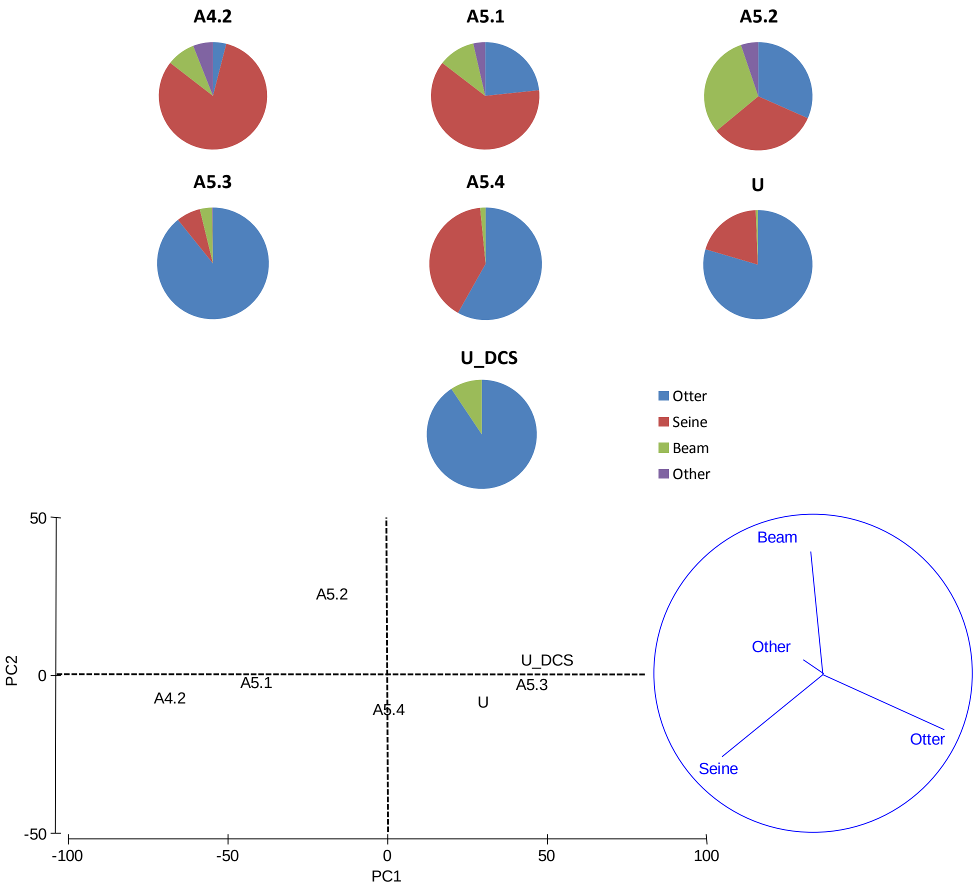


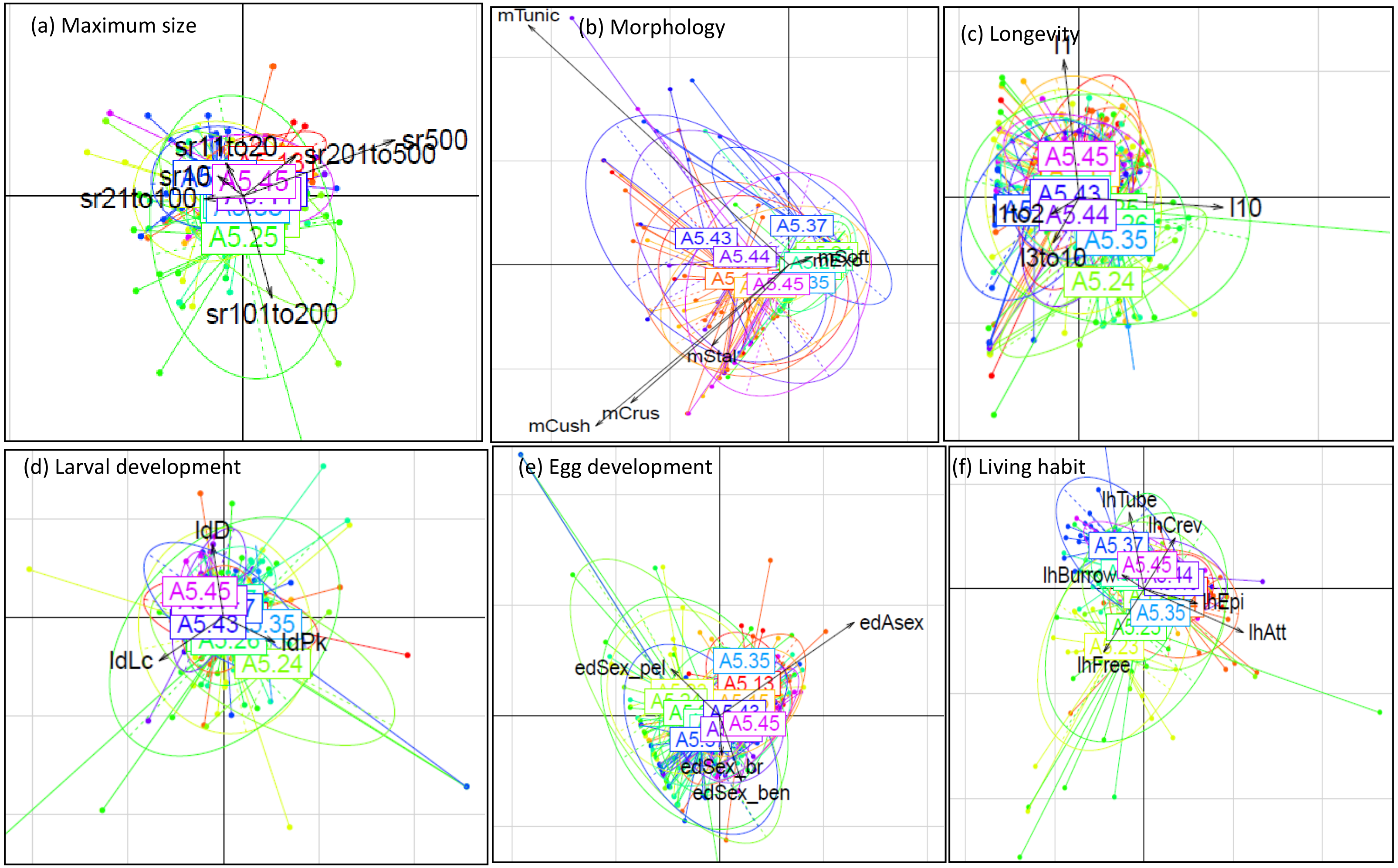
Figure 10. Relative contribution of the various gear types to total FP for epifaunal sampling stations across each EUNIS habitat (top) and 2-d ordination of the relative similarity between habitats following PCA (bottom). Data for habitats for which the traits assemblages were not analysed due to insufficient numbers of stations (Table 5) are not shown. Category 'other' includes a range of gear types but principally various types of dredges.

3.2 Relationship between trait composition and habitats

3.2.1 Infaunal stations

3.2.1.1 EUNIS habitats

The relative differences in trait compositions of the stations estimated as having no- or low FP for each EUNIS habitat are presented in Figures 11(a-j). The overriding feature of these plots is that there is a large amount of within-habitat variability in trait composition, with many stations being significantly separated from their associated habitat centroid. There are some trait compositional habitat differences, although these are both habitat- and trait-specific. There is no clear separation between the habitat centroids for any EUNIS habitat for traits such as sediment position (Figure 11(g)), feeding mode (Figure 11(h)) and mobility (Figure 11(i)). This implies that, under no or low-fished conditions, the numerical compositions of the trait categories do not significantly vary between these EUNIS habitats. Other traits, however, such as morphology (Figure 11(b)), longevity (Figure 9(c)), larval development (Figure 11(d)) and bioturbation mode (Figure 11(j)), display significant variations across habitats. The centroids of some habitats within these four traits possessed a Euclidean separation greater than two, and thus are considered to display significant trait composition habitat differences. The nature of these differences is outlined in Table 7.


(a) Maximum size
sr11to20
sr201to500
sr500
sr10
sr21to100
A5.45
A5.25
sr101to200
(b) Morphology
mTunic
A5.37
A5.43
A5.44
mSoft
A5.45
mStal
mCrus
mCush
(c) Longevity
l1
A5.45
A5.43
l1to2
A5.44
l10
A5.35
l3to10
A5.24
(d) Larval development
ldD
A5.45
A5.43
ldPk
ldLc
A5.24
(e) Egg development
edAsex
A5.35
edSex_pel
A5.13
A5.45
edSex_br
edSex_ben
(f) Living habit
lhTube
lhCrev
A5.37
A5.45
lhBurrow
lhEpi
A5.35
lhAtt
lhFree

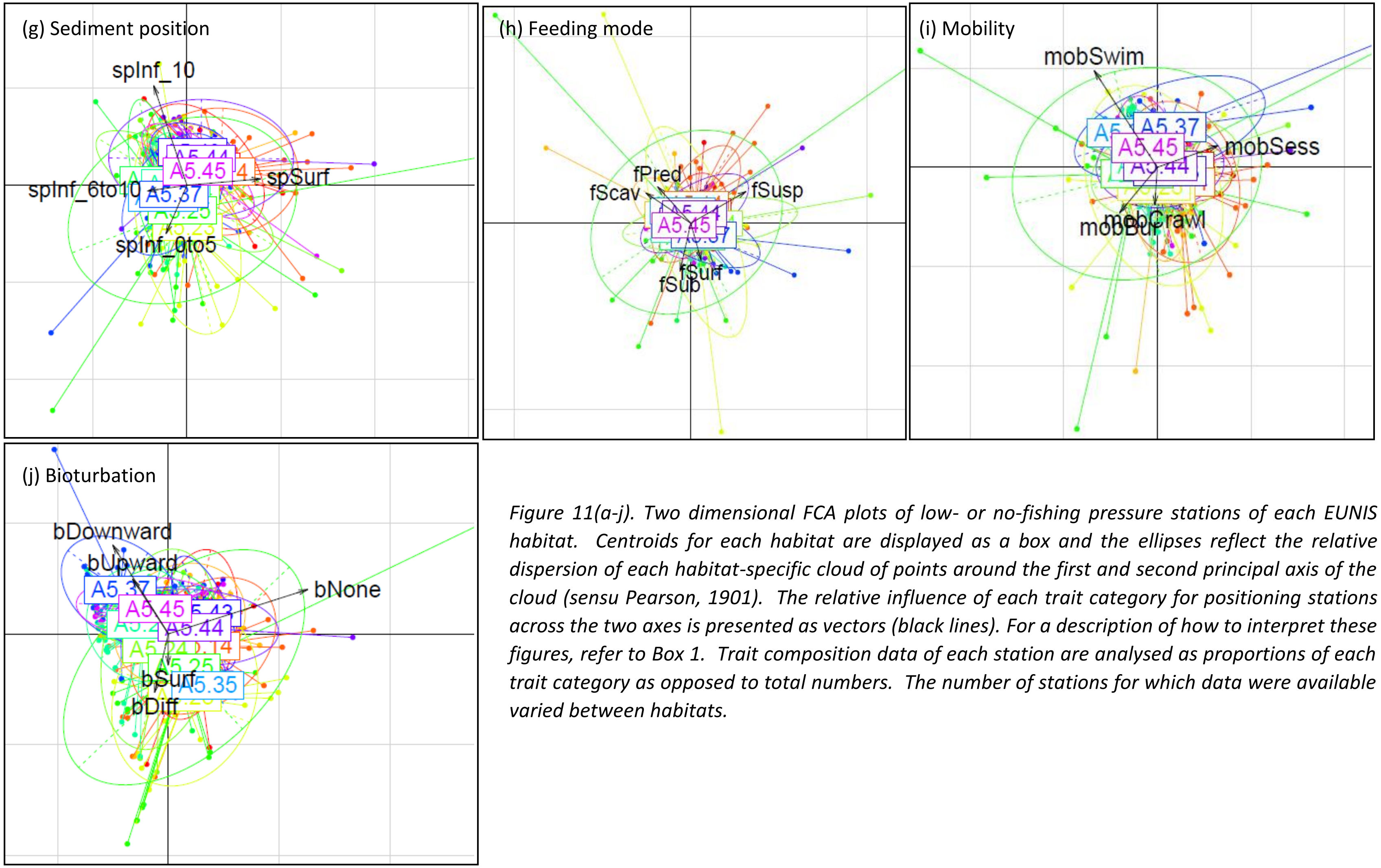


Figure 11(a-j). Two dimensional FCA plots of low- or no-fishing pressure stations of each EUNIS habitat. Centroids for each habitat are displayed as a box and the ellipses reflect the relative dispersion of each habitat-specific cloud of points around the first and second principal axis of the cloud (sensu Pearson, 1901). The relative influence of each trait category for positioning stations across the two axes is presented as vectors (black lines). For a description of how to interpret these figures, refer to Box 1. Trait composition data of each station are analysed as proportions of each trait category as opposed to total numbers. The number of stations for which data were available varied between habitats.

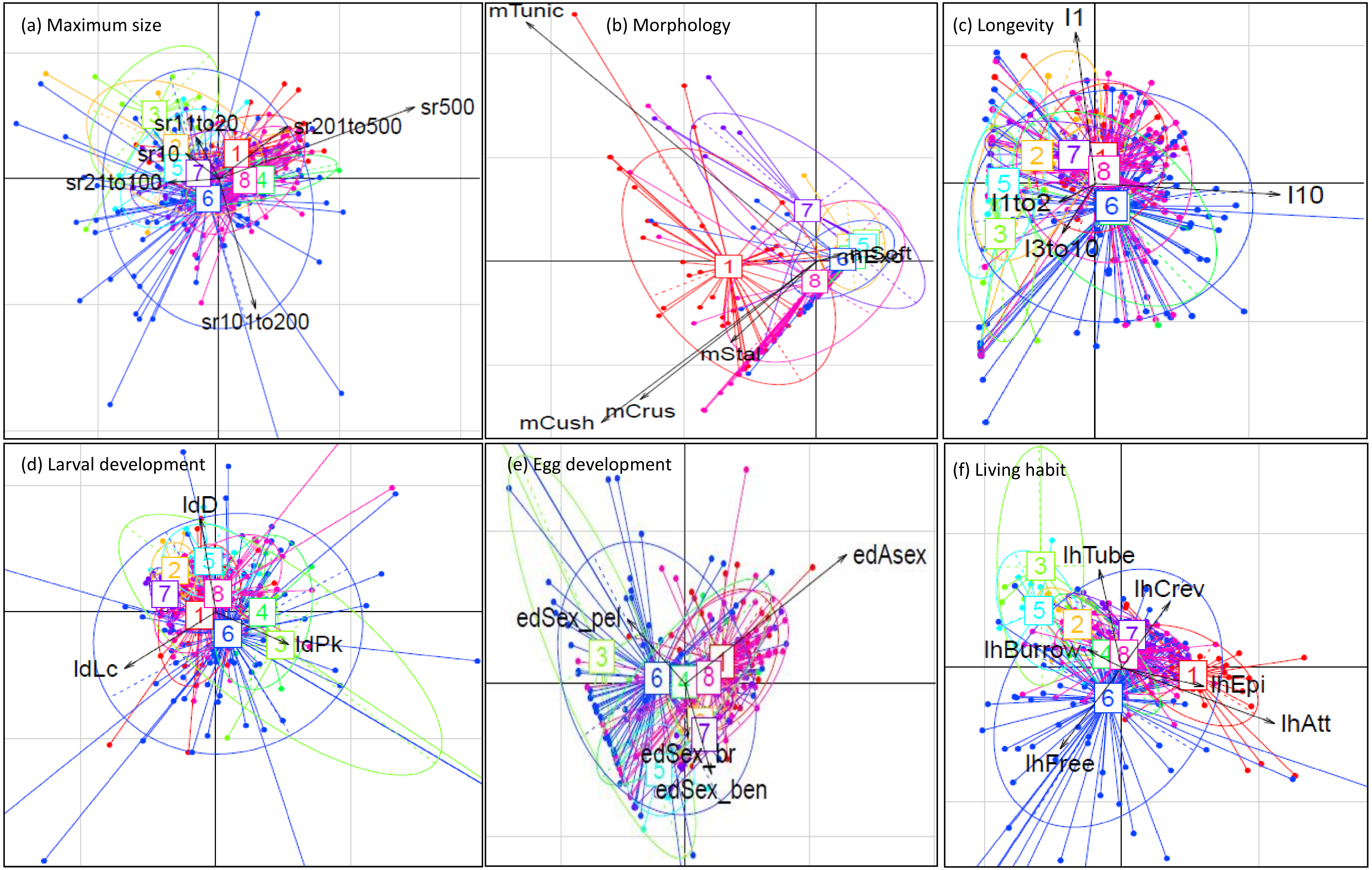
Table 7. Summary of differences in trait composition between EUNIS habitat assemblages. Differences between assemblages are based on those where Euclidean distances between centroids are greater than two (see Figures 9(i-j)). Trait composition data of each station are analysed as proportions of each trait category as opposed to total numbers. The number of stations for which data were available varied between habitats.

Trait	**Cluster groups different**	**Trait category differences**
Maximum size		
Morphology	A5.24 and A5.43	A5.43 (infralittoral mixed sediments) has ↑ tunics
Longevity	A5.24 and A5.45	A5.45 (deep circalittoral mixed sediments) has ↑ <1y
Larval development	A5.24 and A5.45	A5.24 (infralittoral muddy sand) has ↑ planktonic larval producers; A5.45 (deep circalittoral mixed sediments) ↑ direct developers
Egg development		
Living habit		
Sediment position		
Feeding		
Mobility		
Bioturbation	A5.37 and A5.23 A5.37 and A5.35	A5.37 (deep circalittoral mud) has ↑ upwards and downward conveyors; A5.23 (infralittoral fine sand) and A5.35 (circalittoral sandy mud) has ↑ surface depositors and diffusive mixers

3.2.1.2 K-means cluster habitats

The FCA plots of the trait compositions of the stations grouped according to their k-means cluster groups are presented in Figures 12(a-j) and the nature of any significant differences in trait composition is displayed in Table 8. The relative trait composition specificity to cluster groups varies between traits, i.e., while trait category compositions for longevity, larval development and egg development show no significant variation between habitats, there is significant variability for the other traits. Bioturbation, in particular, shows the greatest habitat specificity. This implies, on the assumption that trait composition variation represents functional variation, that under no- or low fishing pressure, assemblages of certain cluster-based habitats do vary in their functional characteristics. Assemblages of Cluster 3 from the very deep cold and slightly sandy mud areas of the Norwegian shelf, in particular, show the greatest trait composition difference from those of the other habitats, possessing elevated proportions of smaller, sessile, tube-dwellers and upward and downward conveyors. Interestingly, the geographically similar assemblages of Cluster 2, which are found in less muddy, slightly shallower areas, do not display any trait composition difference from any other habitat. To note, however, that these two clusters (together with Cluster 5) were represented by the fewest stations and, thus, having excluded the medium and high-FP stations, the remaining stations were unable to sufficiently reflect the traits composition of the no- or low-FP assemblages for these clusters.

It is evident that when the stations are categorised by k-means cluster groups as opposed to EUNIS habitats, the trait composition differences between habitats are greater. This would indicate that k-means cluster groups define environmental groups that encapsulate functional variability better than that shown by EUNIS groups, even though the EUNIS classes used represent those refined in accordance with their observed sediment granulometric characteristics. This result has potentially significant implications for the use of the current EUNIS classification in support of environmental impact assessments of habitat function.


(a) Maximum size
sr500
sr11to20
sr201to500
sr10
sr21to100
sr101to200
(b) Morphology
mTunic
mSoft
mExo
mStal
mCush
mCrus
(c) Longevity
l1
l10
l1to2
l3to10
(d) Larval development
ldD
ldPk
ldLc
(e) Egg development
edAsex
edSex_pel
edSex_br
edSex_ben
(f) Living habit
lhTube
lhCrev
lhBurrow
lhEpi
lhAtt
lhFree
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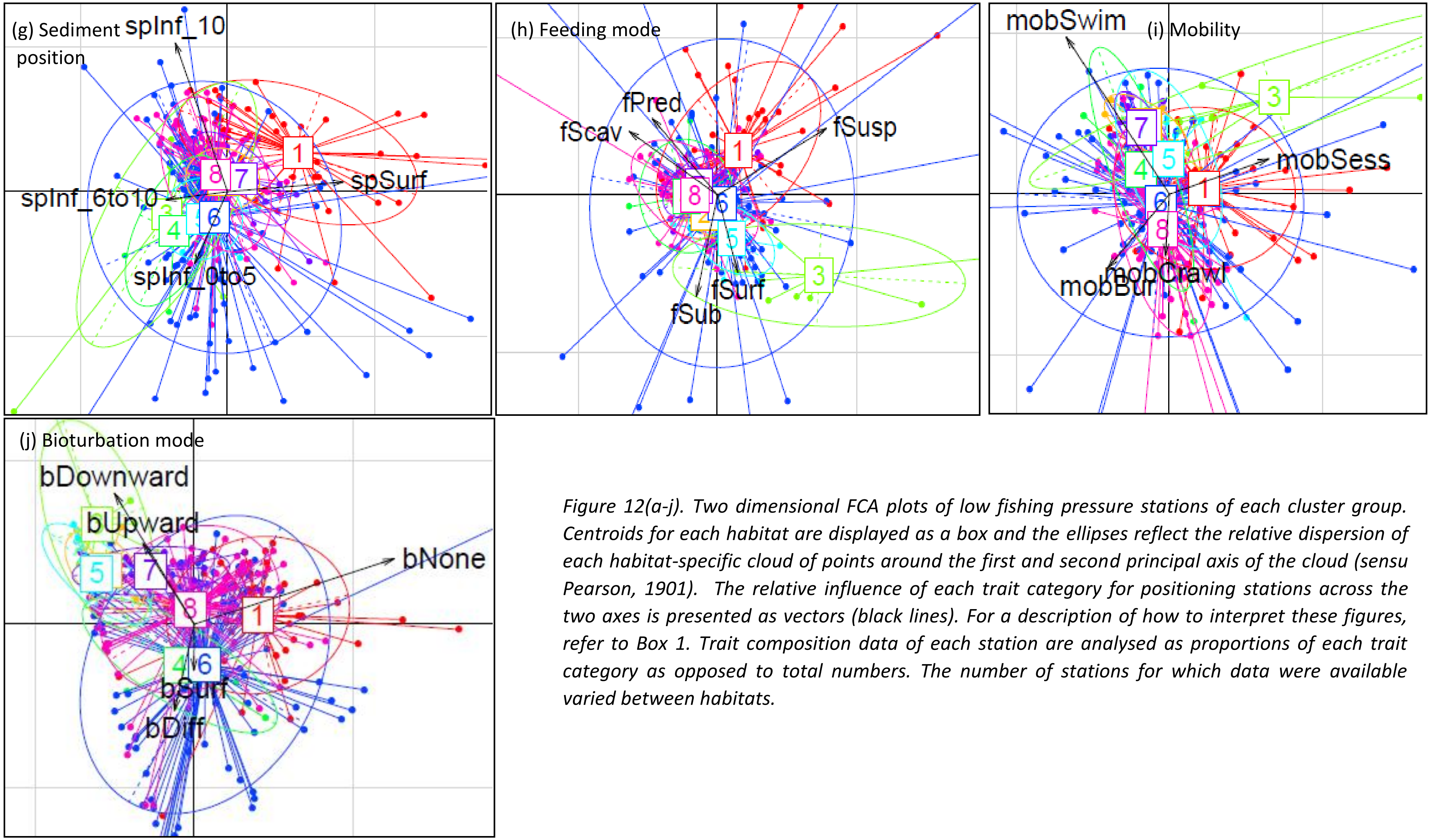

Figure 12(a-j). Two dimensional FCA plots of low fishing pressure stations of each cluster group. Centroids for each habitat are displayed as a box and the ellipses reflect the relative dispersion of each habitat-specific cloud of points around the first and second principal axis of the cloud (sensu Pearson, 1901). The relative influence of each trait category for positioning stations across the two axes is presented as vectors (black lines). For a description of how to interpret these figures, refer to Box 1. Trait composition data of each station are analysed as proportions of each trait category as opposed to total numbers. The number of stations for which data were available varied between habitats.

Table 8. Summary of trait differences between assemblages of Clusters 1 – 8. Differences between cluster groups are based on those where Euclidean distances between centroids are greater than two (see Figures 12(a-j)). Trait composition data of each station are analysed as proportions of each trait category as opposed to total numbers. The number of stations for which data were available varied between habitats.

Trait	Cluster groups different	Trait category differences
Maximum size	3 and 4	Cluster 3 greater composition of small sizes (<10mm, 11-20mm), Cluster 4 more dominated by larger sizes (201-500mm, >500mm)
Morphology	1 and 3, 5	Cluster 1 more dominated by cushioned and crustose organisms than those of Clusters 3 and 5
Longevity		
Larval development		
Egg development		
Living habit	1 and 3, 5 3 and 6	Assemblages of Cluster 1 are more dominated by epiphytic and attached organisms, Clusters 3 and 5 by tube-dwellers and those of cluster 6 have a greater proportion of free-living individuals
Sediment position	1 and 3, 4	Clusters 3 and 4 more dominated by 0-5cm and 5-10cm sediment depth than assemblages of cluster 1 which have a greater proportion of surface-dwellers
Feeding	3 and 4, 7, 8	Assemblages of Clusters 4, 7 and 8 have a greater proportion of scavengers and predators than those of Cluster 3, which shows higher proportions of suspension and surface deposit feeders
Mobility	3 and 6, 8	Assemblages of Cluster 3 exhibit a greater proportion of sessile organisms compared to those of Clusters 6 and 8
Bioturbation	1 and 2, 3, 5 3 and 4, 6	Cluster 1 has a greater proportion of non-bioturbators, downward and upwards conveyors are more dominant in Clusters 2, 3 and 5, while biodiffusers and surficial depositors assume greater compositions in Clusters 4 and 6.

3.2.2 Epifaunal stations

The FCA plots of the no- or low FP stations reveal that, in common with the situation observed for the infaunal stations, the degree of habitat specificity of epifaunal assemblage trait composition is very trait-dependent. While trait composition did now show any habitat relationships for most traits, epifaunal assemblages varied between habitats with respect to larval development, living habit and protection (Figures 13d, f and k). The Euclidean separation between certain habitat centroids was > 1.5 for these three biological traits. However, it is evident that, even for these traits, most habitats did not display any significant trait compositional differences. Regarding larval development, differences were attributable to assemblages of A5.1 (sublittoral coarse sediment) displaying greater proportion of planktonic larval producers than A5.4 (sublittoral mixed sediments) and U_DCS (deep circalittoral seabed), those of A5.2 (sublittoral sand) comprising more planktonic larval producers and A5.4 tending to contain a greater proportion of lecithotrophic larval producers (Table 9).

Clearly, therefore, as with infaunal assemblages, there is a wide variability in the trait composition for all ten traits within any habitat, this within-habitat variability is generally greater than any between-habitat differences.

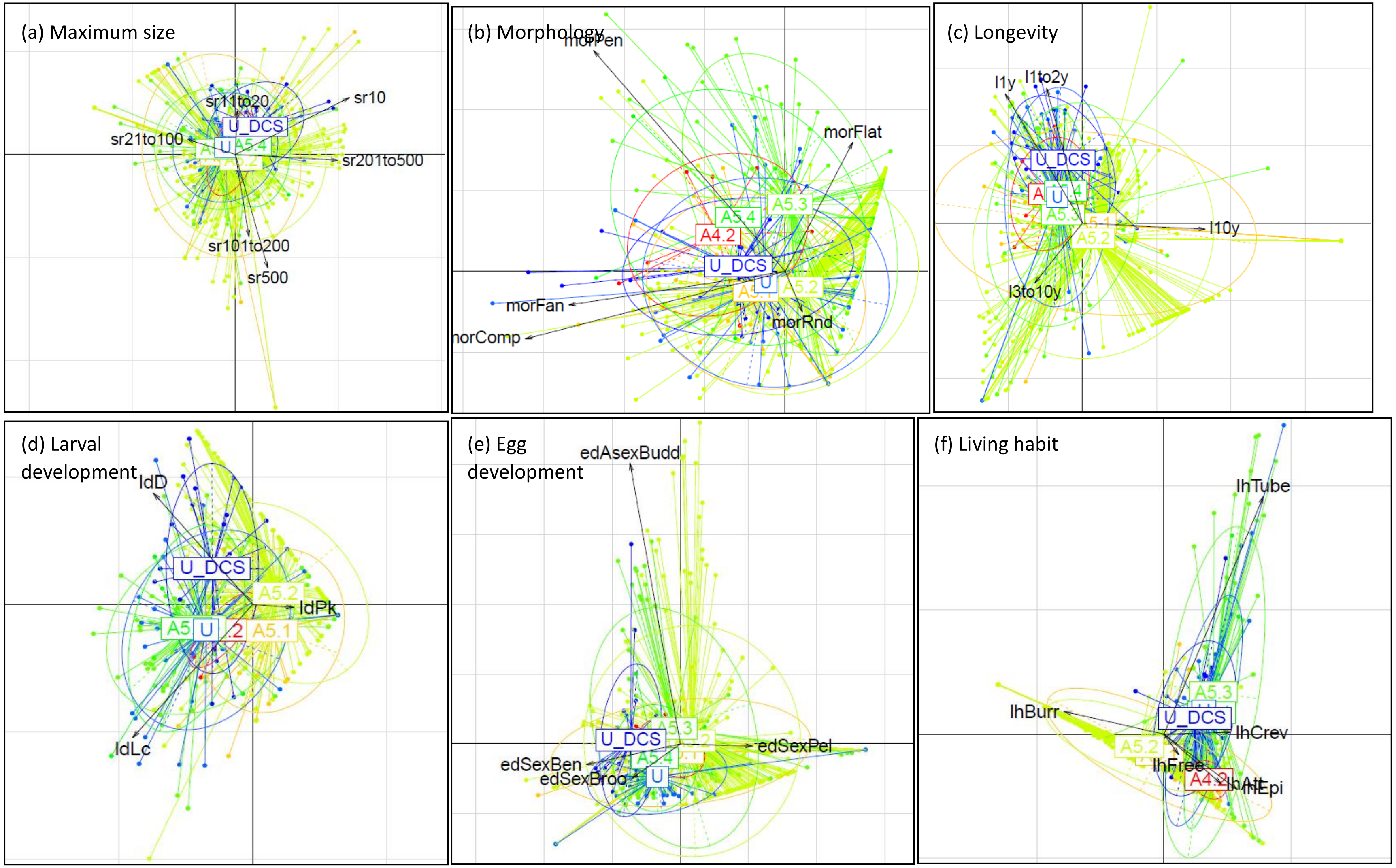
(a) Maximum size
sr11to20
sr10
U_DCS
sr21to100
U
A5.4
sr201to500
sr101to200
sr500
(b) Morphology
morPen
morFlat
A5.4
A5.3
A4.2
U_DCS
U
A5.2
morFan
morComp
morRnd
(c) Longevity
l1y
l1to2y
U_DCS
A
U
A5.3
A5.2
l10y
l3to10y
(d) Larval development
ldD
U_DCS
A5.2
ldPk
A5
U
2
A5.1
ldLc
(e) Egg development
edAsexBudd
A5.3
U_DCS
edSexPel
edSexBen
edSexBroo
A5.4
U
(f) Living habit
lhTube
A5.3
lhBurr
U_DCS
lhCrev
A5.2
lhFree
A4.2
lhAtt
lhEpi

Figure 13(a-l). Two dimensional FCA plots of stations (by EUNIS habitat) estimated to have no or low fishing pressure. Centroids for each habitat are displayed as a box and the ellipses reflect the relative dispersion of each habitat-specific cloud of points around the first and second principal axis of the cloud (sensu Pearson, 1901). The relative influence of each trait category for positioning stations across the two axes is presented as vectors (black lines). For a description of how to interpret these figures, refer to Box 1. Trait composition data of each station are analysed as proportions of each trait category as opposed to total numbers. The number of stations for which data were available varied between habitats.

Table 9. Summary of trait differences between epifaunal assemblages of the various EUNIS habitats. Differences between assemblages are based on those where Euclidean distances between centroids are >1.5 (see Figures 13(a-l)). Trait composition data of each station are analysed as proportions of each trait category as opposed to total numbers. The number of stations for which data were available varied between habitats.

Trait	**EUNIS differences**	**Trait category differences**
Maximum size		
Morphology		
Longevity		
Larval development	A5.1 and A5.4, U_DCS A5.2 and A5.3, A5.4	A5.1 (sublittoral coarse sediment) has a greater proportion of planktonic larval producers than A5.4 (sublittoral mixed sediment) and U_DCS (deep circalittoral seabed; which is more dominated by direct developers). A5.3 (sublittoral mud) and A5.4 have a greater proportion of lecithrotrophic larval producers than A5.2 (sublittoral sand)
Egg development		
Living habit	A5.3 and A4.2, A5.1, A5.2 A5.2 and A5.4	A5.3 has a greater proportion of tube-dwellers than A4.2 (Atlantic and Mediterranean moderate energy circalittoral rock) which has a greater proportion of attached and epiphytic organisms, A5.1 and A5.2 (greater proportion of burrowers). A5.2 has a greater proprtion of burrowers than A5.4 which is more dominated by tube-dwellers.
Sediment position		
Feeding		
Mobility		
Bioturbation		
Protection	A5.2 and A5.3, A5.4, U, U_UDCS A5.1 and A5.4	A5.2 has a greater proportion of robust organisms compared to A5.4, U and U_DCS which have greater proportions of unprotected individuals. A5.1 has a greater proportion of skin/exoskeleton individuals.
Bed/reef		

3.3 Effects of fishing on traits

3.3.1 Infaunal stations

3.3.1.1 EUNIS habitats

The numerical analysis to determine the effects of fishing on trait composition was undertaken using data from all sampling stations, i.e., includes those from no- to high FP estimates. The resulting FCA revealed that assemblage composition of the trait categories displayed specific relationships with FP. FP vector lengths within the FCA plots showed large differences between EUNIS habitats (Table 10). These vectors were relatively long for some EUNIS habitats such as A5.35 (circalittoral sandy mud), A5.37 (deep circalittoral mud), A5.43 (infralittoral mixed sediments) and A5.44 (circalittoral mixed sediments), while relatively short for others such as A5.15 (deep circalittoral coarse sediments). This observation does not appear to be associated with the distribution of FP values across the stations for each habitat (see Figure 6 in Section 3.1.2), as the FP metrics for the stations of A5.15, for example, do not appear markedly different from those of other habitats. Furthermore, FP vector length does not appear to relate to numbers of stations within each habitat. It therefore seems that FP vector lengths properly quantify the strength of the relationship between FP metrics and the variability in the relative composition of all trait categories within a trait.

Table 11 reveals that FP is correlated with the trait composition of infaunal assemblages for the majority of habitats; the FCA plots for these being presented in Appendix 2. The assemblages of all habitats showed some significant trait relationships (here defined by the presence of a significant correlation between total FP and proportion of the trait category) with FP, except for A5.45 (deep circalittoral mixed sediments). While the assemblages of some EUNIS habitats displayed significant correlations with FP for a number of trait categories, significant correlation with FP was observed for relatively few trait categories for other EUNIS habitats. This would imply a large habitat difference in the magnitude of trait responses to fishing. The habitat displaying the greatest response (in terms of the number of traits showing significant correlations with FP) was A5.25 (circalittoral fine sand): the composition of nine of the 10 traits showed significant correlations (Table 11). Data from 168 stations were represented for this habitat from three source participants (Cefas, ILVO, IMARES) and the habitat exhibited a FP distribution comparable to the majority of the other habitats (Figure 6). A number of other habitats displayed FP correlations for an almost comparable number of traits (i.e. eight) such as A5.14 (circalittoral coarse sediment), A5.23 (infralittoral fine sand) A5.44 (circalittoral mixed sediments); these habitats were represented by 86, 94 and 24 stations, respectively, and exhibited comparable FP distributions to other habitats. Therefore, the differences in the number of significant correlations observed across the various habitats do not appear to be an artefact associated either with the number of stations sampled, or with differences in FP distributions; they reflect the relative sensitivities of the different habitats to the effects of fishing.

The most common trait category responses were generally negative ones, i.e., fishing tends to lead to significant reductions in certain traits, but less evidently to significant increases in other traits (Table 12). We must remember that, as the data are analysed as proportions of each trait category, the significance of a correlation of a trait is affected by the response of all the other categories within the trait. Increased fishing may be summarised, i.e., across all EUNIS habitats, as resulting in assemblages with reduced numbers of attached, stalked, epiphytic, non-bioturbating organisms and with increases in the proportions of free-living individuals. Since the traits listed in Table 12 depict only those traits showing the highest number of significant correlations across the 13 EUNIS habitats, one should appreciate that not all habitats respond according to this generalisation, there are, indeed, appreciable inter-habitat differences.

It is interesting to compare the nature of the trait responses to FP between habitats. For example, while the majority of trait categories displayed more-or-less consistent responses, a number of traits showed differing responses between habitats. Morphology showed a relatively consistent response with FP: although the response to fishing of soft-bodied individuals and those with an exoskeleton varied between habitats, the proportion of stalked and crustose individuals of infaunal assemblages showed consistently negative correlations with FP. Similarly, within living habitat, proportions of free-living and burrower trait categories often increased with FP, while attached, epiphytic and tube-building individuals consistently showed declining proportions with increasing FP (Table 11). Finally, surface-dwelling (sediment position trait) invertebrates showed negative correlations with increasing FP, while the proportions of non surface-dwelling (i.e. 0 – 5 cm, 5 – 10 cm) individuals showed significant increases across a number of habitats. In contrast, there was little consistency in the manner in which the composition of the various feeding mode trait categories was correlated with FP. While scavengers and surface deposit-feeders increased with FP in two habitats, the proportions of suspension- and sub-surface deposit-feeders displayed opposing trends with FP between habitats.

Table 10. Euclidean lengths of the FP metric vector from the FCA plot of each trait for each EUNIS habitat.

Trait	**A5.13**	**A5.14**	**A5.15**	**A5.23**	**A5.24**	**A5.25**	**A5.26**
	Infralittoral coarse	Circalittoral coarse	Deep circalittoral coarse	Infralittoral fine sand	Infralittoral muddy sand	Circalittoral fine sand	Circalittoral muddy sand
Maximum size	3.6	0.8	0.1	1.8	0.6	0.2	2.8
Morphology	2.6	0.5	0.1	1.1	0.9	1.1	1.1
Longevity	3.2	1.6	0.2	0.9	1.0	0.6	3.4
Larval development	3.7	1.5	0.5	2.4	1.6	1.3	2.0
Egg development	4.7	0.3	0.2	1.2	1.2	1.2	2.0
Living habit	4.8	0.7	0.4	1.3	1.5	1.6	3.5
Sediment position	2.4	1.0	0.3	0.1	1.0	1.3	2.3
Feeding mode	3.4	1.3	0.1	1.2	1.1	0.4	3.3
Mobility	2.2	0.5	0.2	0.6	1.5	0.4	2.9
Bioturbation	3.6	0.3	0.3	1.4	1.1	1.4	1.9

Trait	**A5.27**	**A5.35**	**A5.37**	**A5.43**	**A5.44**	**A5.45**
	Deep circalittoral sand	Circralittoral sandy mud	Deep circalittoral mud	Infralittoral mixed	Circalittoral mixed	Deep circalittoral mixed
Maximum size	1.1	14.5	6.7	5.6	5.9	1.1
Morphology	0.9	15.3	3.0	3.6	5.6	1.0
Longevity	1.8	13.6	3.1	6.9	6.0	1.3
Larval development	0.3	11.7	5.1	6.1	5.0	0.5
Egg development	0.6	14.4	0.4	5.8	5.7	0.8
Living habit	2.7	7.2	9.8	6.9	5.8	0.5
Sediment position	1.9	11.2	3.3	7.5	6.3	0.1
Feeding mode	1.1	4.5	8.2	7.1	6.1	0.2
Mobility	2.2	17.8	6.5	6.9	4.1	0.6
Bioturbation	1.1	13.2	9.2	6.1	5.6	0.8

*Table 11. Significant Spearman rank correlation coefficients between FP and the proportions of each trait category within each trait. ↑ denotes proportion of trait category within the assemblage increases in stations with increasing FP (positive correlation) while ↓ denotes trait category shows a declining proportion within the assemblage with increasing FP (negative correlation). The correlation coefficient values are prefixed with asterisks to indicate the significance of the correlation coefficient: * p<0.05; **p<0.01.*

EUNIS	**Maximum size**	**Morphology**	**Longevity**	**Larval devel.**	**Egg devel.**	**Living habit**	**Sediment position**	**Feeding mode**	**Mobility**	**Bioturbation mode**
A5.13	↑ <10mm *0.47 ↓ 11-20mm **-0.65 ↓ 201-500mm **-0.62 ↓>500mm **-0.53	↓ crustose *-0.52 ↓ stalked *-0.47			↓ asexual **-0.60	↑ free-living **0.72 ↓ crevice **-0.73 ↓ attached **-0.56	↑ 0-5cm *0.47 ↑ 5-10cm *0.55 ↓ surface **-0.50		↑ swimmers *0.48 ↑ burrowers **0.61 ↓ sessile *-0.48	↑ diffusive mix. **0.73 ↓ surf. Deposit. *-0.50 ↓ none *-0.46
A5.14		↑ soft **0.31 ↓ exoskeleton **-0.34	↑ 1-2y **0.35 ↓ 3-10y **-0.41	↓ planktonic *-0.23		↑ free-living *0.28	↑ 6-10cm **0.32 ↓ surface *-0.22	↑ sub-surface **0.30 ↑ scavenger *0.26 ↓ suspension **-0.32	↑ swimmers *0.22	↑ diffusive mix. **0.36 ↓ surf deposit **-0.38
A5.15		↑ exoskeleton **0.40 ↓ soft **-0.39				↑ free-living *0.33 ↓ tube-builders **-0.46			↓ sessile *-0.31	↓ upward conv. **-0.43
A5.23	↓ 11-20mm **-0.44 ↓ 201-500mm **-0.42	↓ stalked **-0.33	↓ 1-2y *-0.24	↑ planktonic **0.30 ↓lecithotrophic **-0.54	↓ asexual **-0.28	↓ epiphytes **-0.27 ↓ attached **-0.34		↓ subsurf. Dep. *-0.25		↓ upward. Conv. *-0.21 ↓ none **-0.35
A5.24					↓ pelagic eggs *-0.57					
A5.25	↑ <10mm **0.22 ↓ 21-100mm *-0.18 ↓ >500mm *-0.18	↓ stalked **-0.31	↑ 1-2y *0.24 ↓ >10y *-0.17	↑ direct **0.29 ↓lecithotrophic **-0.27	↑ brooders **0.25 ↓ asexual **-0.22 ↓ pelagic *-0.18	↑ free-living **0.26 ↓ epiphytes **-0.22 ↓ attached **-0.37		↓ suspension *-0.16	↑ swimmers **0.30	↓ downw. Conv. **-0.20 ↓ none **-0.29
A5.26	↓ <10mm *-0.33	↓ stalked *-0.27	↓ 3-10y *-0.34	↓lecithotrophic *-0.27	↓ asexual *-0.26	↓ crevice *-0.28		↑ suspension **0.37 ↓ surface *-0.29 ↓ sub-surf. *-0.28		
A5.27	↓ 201-500mm					↑ burrowers	↑ 0-5cm		↓ burrowers	

	*-0.17					**0.22 ↓ epiphytes **-0.2 ↓ attached *-0.16	*0.16 ↓ surface **-0.25		*-0.15	
A5.35	↓ 201-500mm *-0.63 ↓ >500mm *-0.77	↓ stalked **-0.78	↓ <1y *-0.64			↓ attached **-0.76 ↓ epiphytes **-0.76	↑ 6-10cm **0.72 ↓ surface *-0.69 ↓ >10cm *-0.63			↓ none **-0.78
A5.37	↑ 101-200mm *0.4 ↑ >500mm **0.47	↑ exoskeleton *0.27	↑ 3-10y **0.33 ↓ 1-2y **-0.44			↑ free-living *0.43 ↑ burrowers *0.27 ↑ epiphytes *0.30 ↓ tube-builders **-0.72		↑ predators **0.60 ↑ scavengers **0.48 ↓ suspension **-0.51	↑ burrowers **0.49 ↑ crawlers **0.39 ↓ sessile **0.56	↑ surficial dep. *0.31 ↓ down.conv. **-0.73
A5.43	↓ 11-20mm *-0.62		↑ >10y **0.77 ↓ 3-10y *-0.63		↓ brooders **-0.75					↓ down.conv. **-0.73
A5.44	↑ 21-100mm **0.70 ↓ <10mm *-0.42 ↓11-20mm *-0.49 ↓ 101-200mm **-0.56	↓ tunic *-0.46 ↓ crustose *-0.45	↓ 3-10y **-0.60			↓ attached *-0.40 ↓ epiphytes *-0.43	↑ 6-10cm *0.49	↓ surface dep. **-0.60	↓ swimmers **-0.58	↓ none *-0.48
A5.45										

Table 12. Trait categories showing the highest number of significant correlations with total FP across the 13 EUNIS habitats for the infaunal assemblages. ↑ denotes a positive correlation while ↓ denotes a negative correlation.

Trait	Trait category		No. habitats
living habit	attached	↓	6
morphology	stalked	↓	5
living habit	free-living	↑	5
living habit	Epiphytic	↓	5
bioturbation	none	↓	5

3.3.1.2 Cluster groups

The FP vector lengths of the FCA plots of infaunal assemblages when classified by k-means cluster habitats showed large differences between clusters (as was observed between EUNIS habitats) (Table 13). FP vector lengths of Clusters 3, 6 and 7 were generally the shortest and those of Clusters 4 and 5 the longest. Table 14 reveals that the relationship between FP and the percent composition of trait categories of infaunal assemblages is, as was observed for EUNIS habitats, both habitat- and trait-specific (Appendix 1 presents the FCA plots for traits where a significant correlation was observed). While the assemblages of the two somewhat environmentally-similar, Cluster groups 3 (very deep, slightly sandy mud, very low bed flows and temperature) and 5 (deep, muddy or sandy mud, very low bed flow and temperature) showed no significant relationships with FP, the majority of traits displayed some significant correlations with total FP for the assemblages of Clusters 6 (shallow, sandy beds with moderate bed flows and temperature) and 8 (moderate depth, slightly muddy sand, moderate bed flows and warm temperatures). Indeed, the assemblages of Cluster 6 (geographically widely-distributed through the Irish Sea, English Channel, North Sea, Kattegat, Belgian shelf and the Black Sea) showed significant correlations with FP for all biological traits. Note, the distribution of FP estimates for stations of Cluster 6 was essentially comparable to that of other clusters, especially those of 1, 7 and 8.

Despite such habitat-dependency of FP relations with trait composition, there was some consistency in the actual nature of relationships between FP and trait categories, at least for certain traits. For example, within the morphology categories, increased FP values were generally associated with lower numerical compositions of stalked, cushioned and crustose individuals. Living habit also showed relatively consistent relations with FP across the various habitat types, FP being positively correlated with the composition of free-living and burrowing individuals and negatively correlated with attached, tube-building, crevice-dwelling and epiphytic organisms. Finally, FP showed consistent correlations with sediment position trait categories across the various habitat types; percent composition of surface-dwellers being negatively correlated with FP, while those infaunal organisms living at either 0 – 5 cm or 5 – 10 cm sediment depth displayed positive correlations with FP.

However, some traits showed inconsistent relationships with FP across the assemblages of the various cluster habitats. Within the mobility trait, the composition of swimming individuals increased along the FP gradient within the habitats of Clusters 6 and 8, yet it decreased within Cluster 7 and, for feeding mode, the assemblage composition of scavengers increased with FP in Clusters 1 and 6, while it showed a negative relationship within the assemblages of Cluster 8.

Table 13. Euclidean lengths of the FP metric vector from the FCA plot of each trait for each assemblage habitat cluster group.

	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8
	Shallow, gravely sand, strong bed flow	Deep, muddy sand, low temperature and flow	Very deep, slightly sandy mud, very cold	Moderately shallow, sandy mud, warm	Deep, muddy or sandy mud, low flow and very cold	Shallow, sandy, moderate currents	Moderately deep, sandy mud, low flow	Medium depth, slightly muddy sand, warm
Maximum size	2.3	0.9	0.2	5.7	1.5	0.7	1.2	1.4
Morphology	1.2	1.0	0.3	2.6	5.5	1.3	0.4	2.2
Longevity	2.2	1.2	0.1	5.0	1.4	0.7	1.9	1.8
Larval development	2.0	1.1	0.1	3.6	4.8	1.2	1.0	0.8
Egg development	2.0	0.9	0.2	5.0	5.9	0.9	0.6	1.7
Living habit	2.7	1.9	0.3	5.3	4.6	1.2	0.3	3.8
Sediment position	2.6	1.6	0.2	3.7	4.0	0.4	0.4	3.0
Feeding mode	2.0	0.8	0.2	3.3	4.5	0.3	0.4	1.9
Mobility	1.4	0.2	0.3	2.8	1.9	0.8	2.9	3.1
Bioturbation	1.8	2.9	0.2	5.7	6.8	1.1	0.5	2.8

Table 14. Significant Spearman Rank correlation coefficients between FP and traits. ↑ denotes contribution of trait category within the assemblage increases in stations with increasing FP (positive correlation) while ↓ denotes trait category shows a declining contribution within the assemblage with increasing FP (negative correlation). The correlation coefficient values are prefixed with asterisks to indicate the significance of the correlation coefficient: * p<0.05; **p<0.01.

	Maximum size	Morphology	Longevity	Larval devel.	Egg devel.	Living habit	Sediment position	Feeding mode	Mobility	Bioturbation mode
Cluster 1	↓11-20mm **-0.30					↑ burrowers ***0.21 ↓attached **-0.37	↑0-5cm **0.27 ↑6-10cm **0.32 ↓ surface -0.33	↑ scavengers *0.29	↑ burrowers *0.24	↑ diffusive mix **0.33 ↓surf. Dep *-0.24 ↓none *-0.26
Cluster 2								↑subsurf. Dep. *0.53 ↓suspension *-0.59		
Cluster 3										
Cluster 4			↓>10y *-0.28			↓ attached **-0.41	↑6-10cm *0.37	↓ suspension **-0.43		
Cluster 5										
Cluster 6	↓11-20mm **-0.15 ↓201-500mm **-0.13 ↓>500mm **-0.18	↓ stalked **-0.27	↓3-10y *-0.15	↑ Direct **0.14 ↓lecithotrophic **-0.31 ↓ asexual **-0.21	↑ brooders *0.12	↑ free-living **0.17 ↓ attached **-0.27 ↓tube-dwellers **-0.17 ↓epiphytes **-0.23 ↓ crevice **-0.19	↑6-10cm *0.12	↑ scavengers *0.10 ↓surf. Deposit *-0.10	↑ swimmers **0.18	↑ diff. mixers **0.16 ↓ upward. Conv. **-0.23 ↓downw. Conv. **-0.19 ↓ none **-0.25
Cluster 7			↓ <1y *-0.33	↑ planktonic *0.33 ↓ direct *-0.33					↓ swimmers **-0.57	↓ upward conv. **-0.41
Cluster 8	↓ 201-500mm **-0.24	↓ stalked *-0.16 ↓ cushion **-0.26 ↓ crustose **-0.28		↓ asexual **-0.21		↑ burrowers **0.20 ↓ crevice dwell **-0.25 ↓ epiphytes **-0.35 ↓ attached **-0.27	↑ 0-5cm **0.26 ↓ surface **-0.31	↓ scavengers *-0.15 ↓ predators *-0.17	↑ swimmers **0.31 ↓ burrowers *-0.19	↑ surface dep. **0.19 ↓ none **-0.28

The trait categories showing the highest frequency of significant correlations with total FP (Table 15) across the eight cluster groups showed, perhaps not surprisingly, some resemblance with those for the infauna categorised by EUNIS habitat. Increased fishing may be summarised across all cluster group habitats as resulting in assemblages with reduced proportions of attached, non-bioturbating organisms and increases in deeper sediment-dwelling (6 – 10 cm) individuals. Since those traits listed in Table 15 depict only those traits showing the highest number of significant correlations across the eight cluster habitats, one should appreciate that not all habitats respond according to this generalisation, there are, indeed, appreciable inter-habitat differences.

Table 15. Trait categories showing the highest number of significant correlations with total FP across the eight cluster group habitats for the infaunal assemblages. ↑ denotes a positive correlation while ↓ denotes a negative correlation.

Trait	Trait category		No. habitats
living habit	attached	↓	3
sediment position	6 – 10 cm	↑	3
bioturbation	none	↓	3

3.3.2 Epifaunal stations

As was observed for the infaunal assemblage data, the euclidean length of the FP vectors in the FCA plots of the epifaunal assembage data varied widely between habitats (Table 16). While FP vectors were relatively long for EUNIS habitats A5.3 (sublittoral mud; 162 stations) and A5.4 (sublittoral mixed sediment; 20 stations), FP vectors were far shorter across the traits for other habitats, particularly A5.2 (sublittoral sand; 830 stations). Between habitats, the number of traits within which a trait category showed a significant correlation with FP varied from two traits (A4.2, Atlantic and Mediterranean moderate energy circalittoral rock) to all 12 traits (A5.2, sublittoral sand; A5.3, sublittoral mud) (Table 17). Clearly, therefore, as the distribution of FP values for the stations across these habitats were generally comparable, there is a wide disparity in the nature and the relative sensitivities of the assemblage trait compositions to FP between habitats. Appendix 2 displays the FCA plots for those analyses in which a significant correlation between total FP and proportion of a trait category was observed.

For epifaunal assemblages, increased fishing generally (i.e. across all EUNIS habitats) resulted in reduced numbers of attached, flat, tube-building, reef-forming organisms and an increase in round-bodied, burrowing individuals inhabiting deep within (i.e. > 10 cm sediment depth) the sediment matrix. Since those traits listed in Table 18 present only those trait categories with the highest number of significant correlations across the seven EUNIS habitats, one should appreciate that not all habitats respond according to this generalisation, there are, indeed, appreciable inter-habitat differences (as demonstrated in Table 17).

While some traits showed comparatively consistent types of changes along the FP metric gradient, the response of some traits, maximum size, for example, was variable between habitats. The correlations between the various mobility and larval development traits with FP values also showed a similarly inconsistent response with FP. In contrast, where significant correlations between total FP with trait categories of morphology and living habit were observed, the nature of the relationship was largely consistent between habitats. Thus, increasing FP estimates correlated with increases in the numerical proportion of round organisms (e.g., crustaceans, worms, bivalve and gastropod molluscs, most echinoderms) and with decreases in those of complex-, fan- and pen-shaped organisms. With respect to living habitat traits, FP was positively correlated with the composition of burrowing organisms and negatively correlated with the composition of tube-building, attached, crevice or epiphytic organisms.

Table 16. Euclidean lengths of the FP metric vector from the FCA plot of each trait based on the epifaunal assemblage data categorised by EUNIS habitat.

Trait	**A4.2**	**A5.1**	**A5.2**	**A5.3**	**A5.4**	**U**	**U_DCS**
	Atlantic and Mediterranean moderate energy circalittoral rock	Sublittoral coarse sediment	Sublittoral sand	Sublittoral mud	Sublittoral mixed sediments	‘unclassified’ (no data)	Deep circalittoral seabed
Maximum size	1.3	1.8	0.4	3.9	4.4	1.2	0.5
Morphology	0.7	2.1	0.5	4.7	5.8	3.1	1.3
Longevity	1.0	1.3	0.7	5.5	1.9	0.6	0.4
Larval development	3.9	1.8	0.4	2.4	4.7	0.8	1.5
Egg development	2.8	1.3	0.5	4.2	4.7	1.9	1.2
Living habit	2.3	1.4	0.2	4.2	5.2	1.2	1.3
Sediment position	2.3	1.2	0.8	3.9	4.2	1.7	1.2
Feeding mode	1.3	1.3	0.3	0.5	3.9	0.7	0.8
Mobility	2.0	1.3	0.8	1.7	5.4	0.1	0.5
Bioturbation	2.2	1.1	0.6	4.4	4.7	1.5	2.0
Fragility	2.9	1.5	0.2	4.3	2.8	0.7	1.3
Bed modifier	0.9	3.0	0.5	3.0	1.6	1.5	1.4

Table 17. Significant Spearman rank correlation coefficients between FP and traits for epifaunal assemblages. ↑ denotes contribution of trait category within the assemblage increases in stations with increasing FP (positive correlation) while ↓ denotes trait category shows a declining contribution within the assemblage with increasing FP (negative correlation). The correlation coefficient values are prefixed with asterisks to indicate the significance of the correlation coefficient: * $p<0.05$; **$p<0.01$.

Habitat	Maximum size	Morphology	Longevity	Larval development	Egg development	Living habit
A4.2				↑lecithotrophic *0.37		
A5.1	↓ 201-500mm *-0.22	↓ fan *-0.25 ↓ complex **-0.29	↓ <1y *-0.22		↑ Pelagic eggs **0.43 ↓ brood eggs **-0.34	
A5.2	↑101-200mm _**0.13_ ↓21-100mm _**-0.20_ _↓ 201-500mm_ _*-0.09_ ↓>500mm _**-0.11_	↑ round **0.12 ↓ complex **-0.2 ↓ fan **-0.14 ↓ pen **-0.13 ↓ flat *-0.08	↑ >10y **0.10 ↓ <1y **-0.11 ↓3-10y **-0.12	↑ planktonic **0.09 ↓ lecithotrophic *-0.08 ↓ direct **-0.11	↑ pelagic eggs **0.14 ↓ brooding **-0.15 ↓ benthic eggs *-0.08 ↓ asexual **-0.15	↑ burrowers *0.09 ↓ tube-builders **-0.12 ↓ attached **-0.14 ↓ epiphytes **-0.18
A5.3	↑<10mm *0.20 ↑ 201-500mm **0.50 ↑ >500mm *0.19 ↓21-100mm *-0.20	↑ round **0.43 ↓ flat **-0.24	↑ <1y **0.45 ↑ 1-2y **0.30 ↓3-10y **-0.25	↓ lecithotrophic *-0.18	↑ brood eggs **0.41 ↑ benthic eggs *0.16 ↓ pelagic eggs **-0.42	↑ burrowers **0.49 ↓ tube-builders **-0.28 ↓ attached **-0.24 ↓ epiphytes *-0.18
A5.4	↓ 11-20mm *-0.5	↑ fan *0.45				↑ epiphytes **0.55
U				↑ direct *0.24 ↓ planktonic *-0.27		↑ crevice *0.28 ↓ tube-builders **-0.28
U_DCS		↑ round **0.48 ↓ flat **-0.50 ↓ complex *-0.31 ↓ fan *-0.30			↓ pelagic eggs **-0.45	↑ burrowers *0.30 ↓ attached *-0.32 ↓ epiphytes *-0.35

Table 17 (Continued).

Habitat	Sediment position	Feeding mode	Mobility	Bioturbation mode	Protection	Bed/reef forming
A4.2					↑ unprotected *0.35	
A5.1	↑ 6-10cm *0.22	↑ suspension *0.26 ↓ predators *-0.23	↑ sessile **0.30 ↓ crawlers *-0.36		↑ robust **0.27 ↑ fragile ***0.46 ↓skin/exoskeleton **-0.33	
A5.2	↑>10cm deep **0.20 ↑ 0-5cm *0.07 ↓ surface **-0.10	↓ predators **-0.14	↑ sessile *0.10 ↓ burrowers **-0.10 ↓ crawlers **-0.17	↑ surficial dep. **0.24 ↓ diffusive mix. *-0.19 ↓ none *-0.19	↑ robust *0.09 ↑ fragile *0.09 ↓ unprotected *-0.08 ↓ skin/exoskeleton **-0.16	↑ none **0.12 ↓ bed-modifiers **-0.16 ↓ reef-formers **-0.15
A5.3	↑>10cm deep ***0.30	↓ scavengers **-0.23	↑ swimmers ***0.31	↑ upward conv. ***0.33	↑ skin/exoskeleton **0.24 ↓fragile ***-0.24	↓ bed-modifiers **-0.25 ↓ reef-formers *-0.21
A5.4			↓ sessile *-0.52			
U	↓ 6-10cm *-0.23	↓ surface dep. **-0.32				
U_DCS	↑>10cm deep **0.43		↑ burrowers *0.30	↑ upward conv. *0.32 ↑ surficial depos. *0.32 ↓ none **-0.41	↑ skin/exoskeleton *0.34 ↓fragile **-0.47	↓ reef-formers **-0.42

Table 18. Trait categories showing the highest number of significant correlations with total FP across the seven EUNIS habitats for the epifaunal assemblages.↑ denotes a positive correlation while ↓ denotes a negative correlation.

Trait	Trait category		No. habitats
Morphology	flat	↓	3
Morphology	round	↑	3
Living habit	tube-builders	↓	3
Living habit	burrowers	↑	3
Living habit	attached	↓	3
Sediment depth	>10 cm	↑	3
Habitat modifiers	Reef-formers	↓	3

3.4 Mapping habitat responses to total FP

3.4.1 Infauna

3.4.1.1 EUNIS habitats

The multivariate analyses of the EUNIS habitat (dis)similarities based on the trait categories, displaying either significant positive or negative correlations with total FP (see Table 11), showed that the infaunal assemblages of some habitats generally responded in comparable ways (see groups A-D; Figure 14). The five EUNIS habitats representing Group A were generally those that showed the largest number of significant correlations with total FP (Table 11); although the actual responses of these habitats varied to some extent, as the proportions of stalked, epifaunal and/or attached, sub-surface desposit-feeding and non-bioturbating organisms showed significant negative correlations with total FP throughout these habitats. Assemblages of those habitats of Group B typically showed fewer correlations between the proportions of traits categories with total FP. Assemblages of A5.13 (infralittoral coarse sediment) and A5.25 (circalittoral fine sand) forming Group D showed significant positive correlations for free-living, small-bodied individuals with total FP and negative correlations for large-bodied (> 500 mm), attached and/or stalked individuals, and non-bioturbating organisms that reproduce *via* asexual development.

Mapping the distribution of the stations according to these groups allows an assessment of the large-scale distribution of the commonalities in trait category responses to total FP (Figure 15). The trait response characterising Group D was only found in the southern North Sea (and a small number of stations in the inshore regions of the English Channel), while that of Groups A to C is found over larger spatial regions.

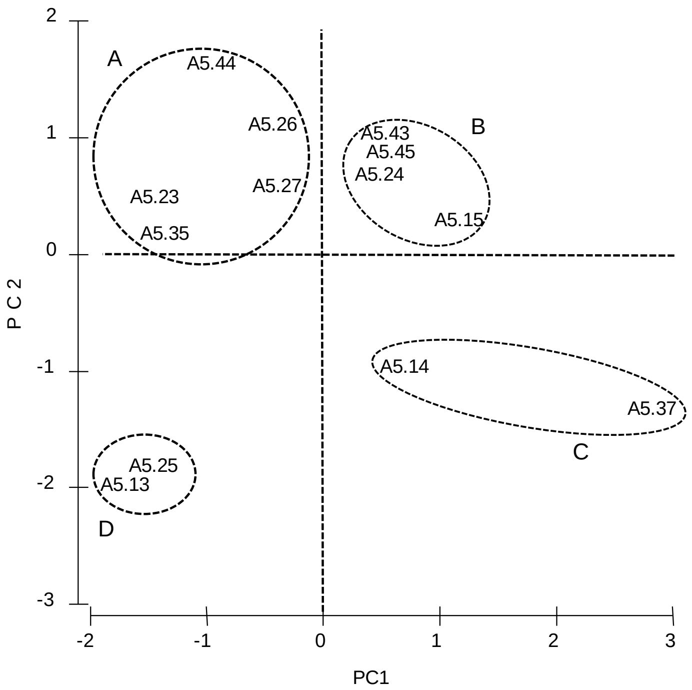

Figure 14. PCA of EUNIS habitats based on significant correlations of trait categories with total FP for infaunal stations. The actual trait category correlations with total FP for each habitat are presented in Table 11.

3.4.1.2 K-means Cluster group habitats

When the infaunal data were categorised into habitat groups derived by k-means clustering, a large proportion of the habitats showed similar responses (Figure 16). Assemblages of Clusters 2, 3, 4, 5 and 7 (Group A; Figure 16) displayed relatively comparable relationships between trait categories and total FP, generally with the absence of a significant relationship with total FP across the 10 traits (Table 14). This type of relationship with total FP was observed across the majority of stations in the northern Norwegian shelf and the small number of stations in the Mediterranean, and at isolated regions in the North Sea, Irish Sea and the Kattegat (Figure 17). Assemblages of the three remaining habitats show different responses; Clusters 6 and 8 displaying a larger number of significant relationships with total FP (Table 14).

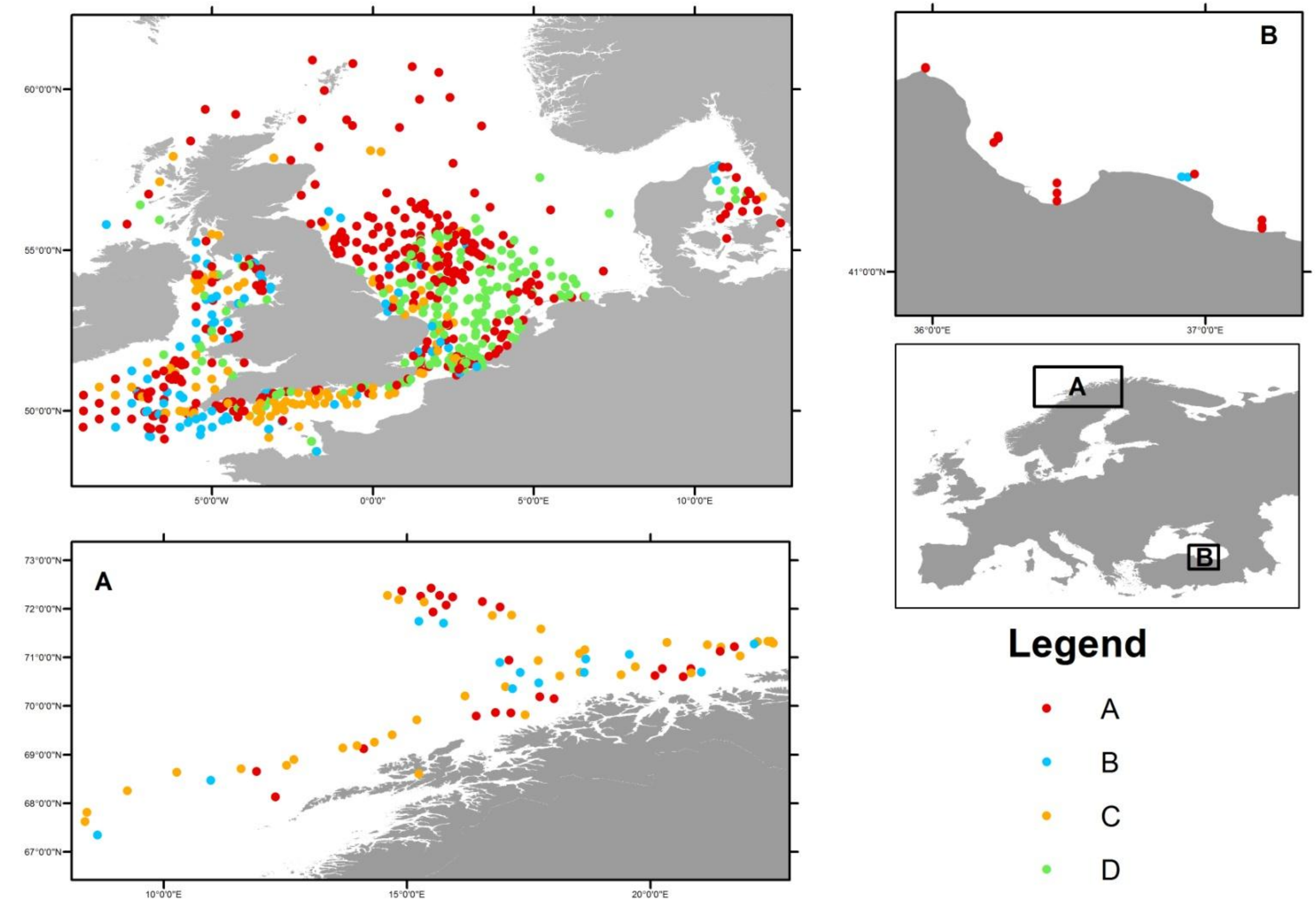

Figure 15. Map showing the distribution of infaunal assemblages, when categorised by EUNIS habitats, showing similar trait composition correlations with total FP. Habitats belonging to Groups A-D are presented in the PCA plot in Figure 14. Note, scale varies between the various insets.

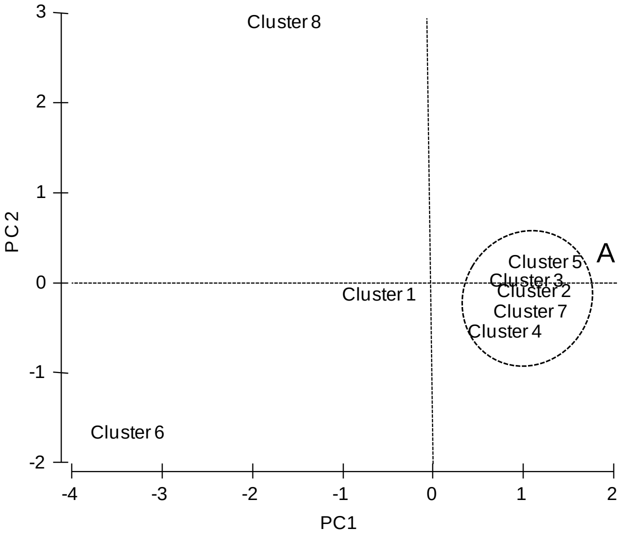

Figure 16. PCA of cluster habitats based on significant correlations of trait categories with total FP for infaunal stations. The actual trait category correlations with total FP for each habitat are presented in Table 14.

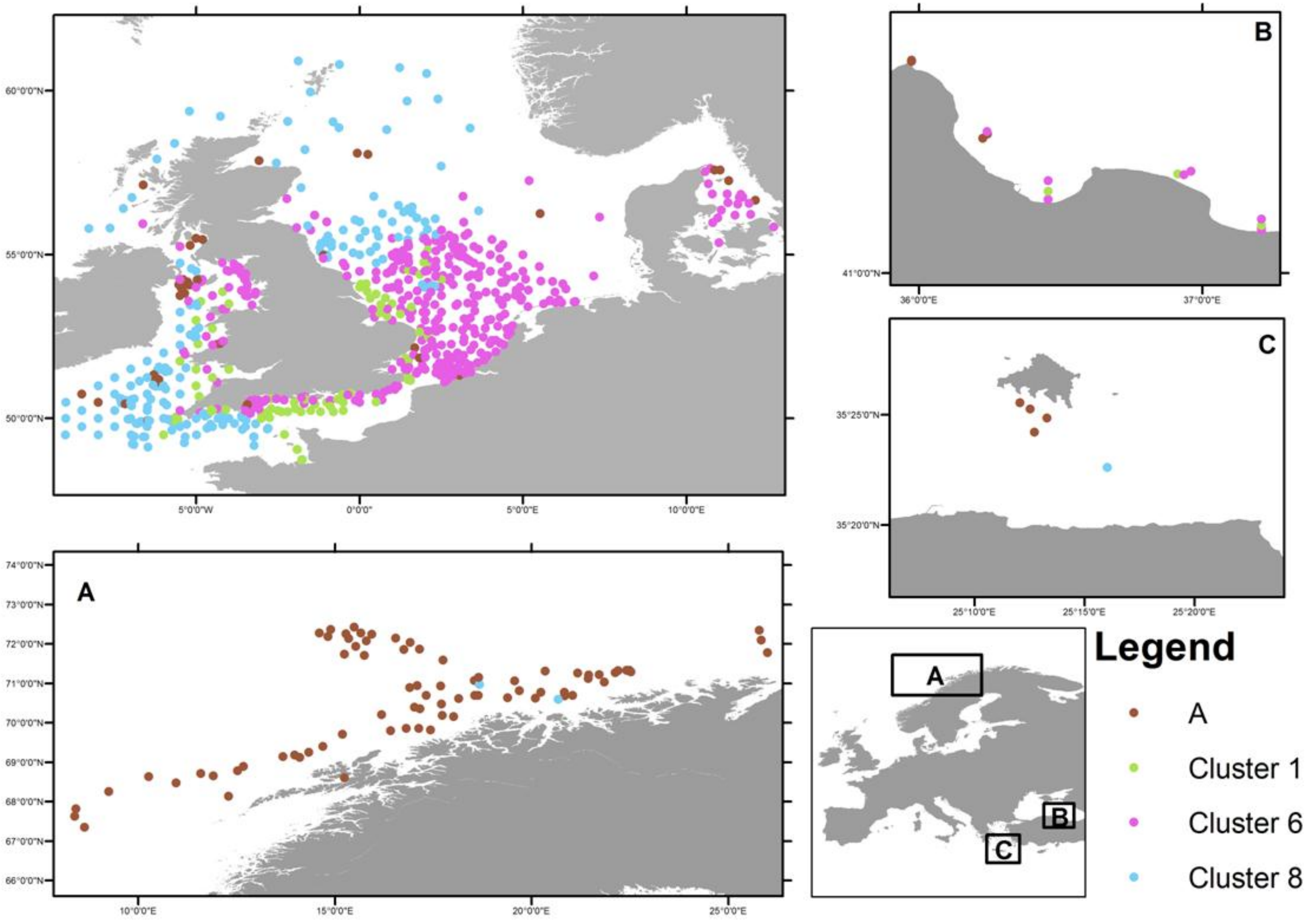

Figure 17. Map showing the distribution of infaunal assemblages, when categorised by k-means Cluster habitats, showing similar trait composition correlations with total FP. Cluster group habitats belonging to Group A are presented in the PCA plot in Figure 16. Note, scale varies between the various insets.

3.4.2 Epifauna

Regarding the epifaunal assemblages, two habitats displayed relatively distinct trait responses to fishing, while the response of the remaining habitats showed some consistent patterns (Groups A and B; Figure 18). Group B response (displayed by A4.2 - Atlantic and Mediterranean moderate energy circalittoral rock; A5.4 - sublittoral mixed sediments; U - unclassified habitats) was typified by very few trait categories having a significant correlation with total FP. Assemblages showing this type of response were located in the Bay of Biscay, across the northern Norwegian shelf, the Mediterranean and the eastern English Channel (Figure 19). Although relatively less consistent in their relationship with fishing, A5.3 (sublittoral mud) and U_DCS (deep circalittoral seabed) (Group A) generally showed positive correlations in round-bodied, burrowing, deep-dwelling (> 10 cm deep), upward conveyor organisms with skin/exoskeleton with total FP, and significant negative correlations in attached, fragile, flat-bodied, reef-forming invertebrates that reproduce *via* pelagic egg production. This response was represented by stations primarily in the Black Sea, northern Norwegian shelf, the Bay of Biscay and the Irish Sea (Figure 19).

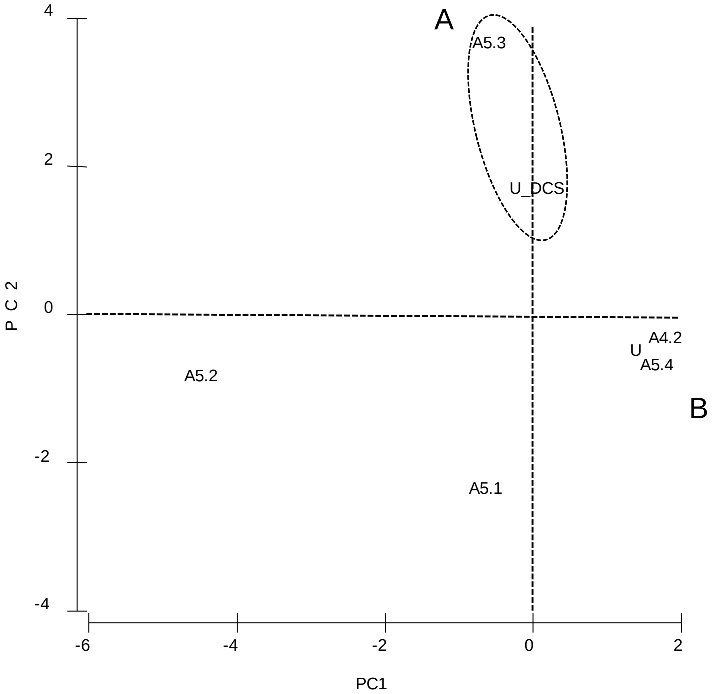

Figure 18. PCA of EUNIS habitats based on significant correlations of trait categories with total FP for epifaunal stations. The actual trait category correlations with total FP for each habitat are presented in Table 17.

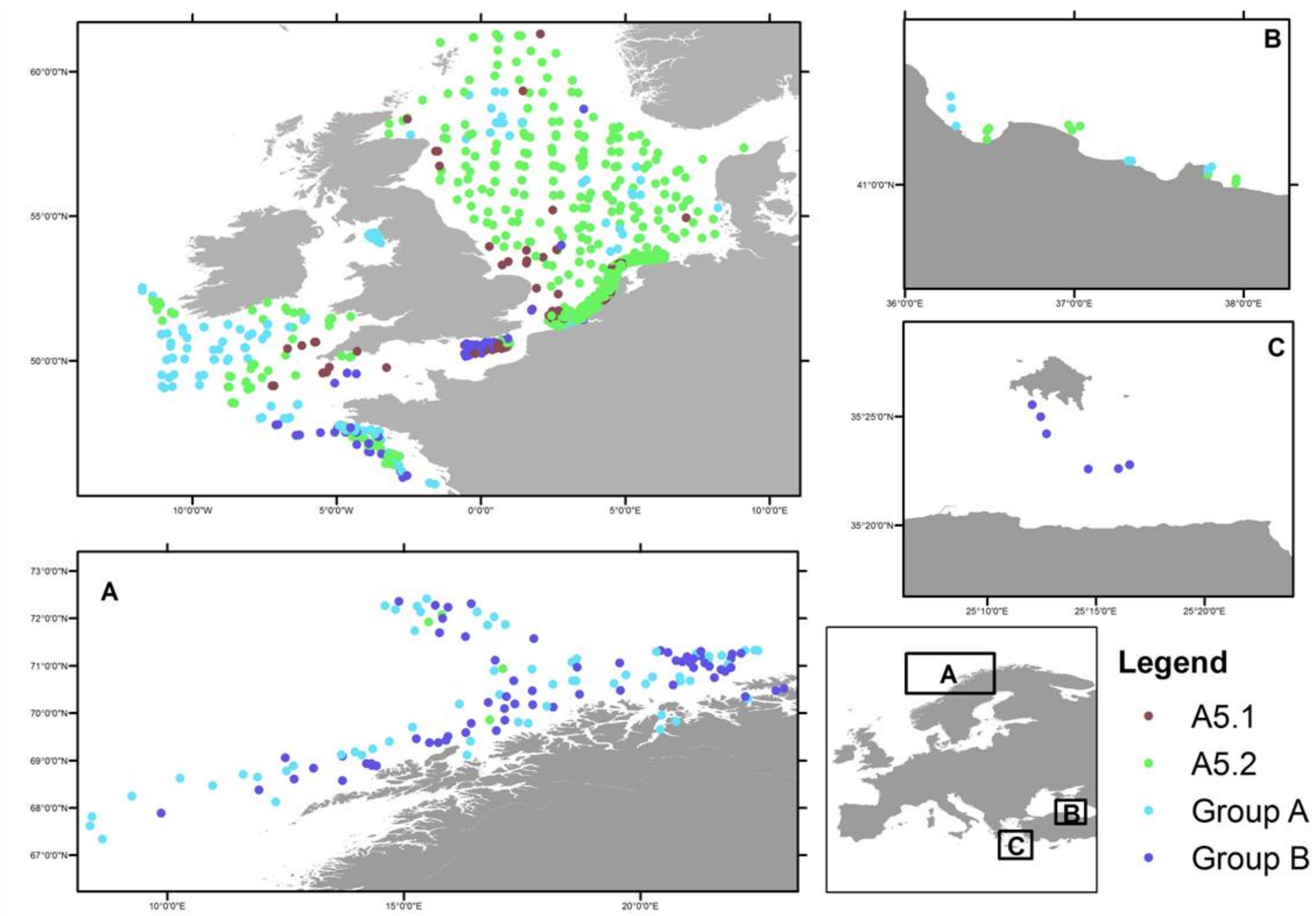

Figure 19. Map showing the distribution of epifaunal assemblages of the various EUNIS habitats showing similar trait composition correlations with total FP. EUNIS habitats represented by Groups A and B are presented in the PCA plot in Figure 18. Note, scale varies between the various insets.

4. DISCUSSION

During the past decade, there have been a number of studies conducted aiming to assess the impact of demersal fishing on the functional characteristics of benthic invertebrate assemblages (e.g. Bremner *et al*., 2005; Tillin *et al*., 2006; Frid 2011; de Juan and Demestre, 2012; Atkinson *et al*., 2012; Fleddum *et al*., 2013). These studies have provided alternative insights regarding fishing impacts on the seabed compared to those assessments focussing on the structural attributes of benthic assemblages. However, the actual methodology in which traits information has been used and analysed has varied widely between studies, and, as a result, it is currently somewhat difficult to draw any useful comparisons regarding both the magnitude and nature of traits effects due to fishing. The inclusion of a much larger number of stations across a wider range of habitats in the present study, compared to those of earlier studies, has enabled a more standardised assessment of the habitat-specificity of fishing impacts on biological traits than hitherto. Furthermore, we believe that investigating biological trait differences based on the composition of each trait separately, as undertaken here, has proved to have a number of advantages over the combined, multi-trait approaches conducted hitherto. Firstly, the results are less dependent upon the choice and/or selection of which traits were included within the study. Secondly, the detection of dissimilarities in the multivariate characteristics of assemblages for one trait is not constrained by the influence of other traits. Finally, determining the actual trait categories displaying marked changes between the various assemblages, either alone or in combination, can subsequently be used to infer independent aspects of functional change more readily.

4.1 Benthic assemblage trait composition of habitats under low/no fishing

When trait compositions of the assemblages under no or low fishing pressure were compared across a wide range of benthic habitats of the European continental shelf, one of the over-riding features of the outcome was the general paucity of clear trait differences between habitats. This observation applied equally to the assemblages of both the infauna and epifauna. The composition of the various trait categories showed very little habitat-variation for any of the ten traits investigated for the infauna or for the 12 traits investigated for the epifaunal assemblages. This finding was perhaps surprising, given the wide differences in the habitats under study. It would have been anticipated, for example, that the deep, cold, low bed-flow conditions prevalent of the deep circalittoral mud habitat (A5.37), or those of Cluster groups 2, 3 and 5 off the Norwegian shelf, would have resulted in significantly different compositions of certain traits, relative to those presenting contrasting environmental conditions (e.g. A5.13 – infralittoral coarse sediment). For example, the vertical distribution of infauna has been shown to be associated with variations in the amount and quality of organic matter reaching the seabed (Dauwe *et al*., 1998) and the environmental conditions prevailing in deep, muddy habitats are deemed unfavourable for suspension-feeding organisms (Pearson and Rosenberg, 1978). Species are adapted to a particular ecological niche (*sensu* Hutchinson, 1957) and, as one species reaches the limits of its niche, then others occur in increasing numbers. Assemblage structure has been shown to significantly vary across a range of habitats and spatial scales far smaller than that of the present study (e.g. Cabioch, 1968; Rees *et al*., 1999; Bolam *et al*., 2008; Somerfield *et al*., 2009; Barrio-Frojan *et al*., 2012). The absence of significant trait composition differences across the habitats within the present study implies that, while various habitats may be defined based on the taxonomic uniqueness of their assemblages, such species changes do not impart significant trait composition changes. This result supports the conclusions of a number of published studies where it has been observed that structural changes in assemblages along environmental or disturbance gradients may not necessarily be accompanied by alterations in benthic functioning (Cooper *et al*., 2008; Barrio-Frojan *et al*., 2011; Sigala *et al*., 2012). Essentially, our results indicate that biological assemblages vary with respect to their trait compositions, however, the large within-habitat variations in trait composition we observed infer that environmental characteristics of the habitats are not, but some other forcing variable(s) are, responsible for such variation. While it is possible that some of this variability may have resulted from methodological differences between source datasets and the choice of the traits, it is likely that it actually reflects variability in some other environmental variables not controlled within the present study.

Despite the general similarity in traits composition between habitats under no or low fishing pressure, some trait differences were discernible. A5.24 (infralittoral muddy sand), for example, contained a much lower numerical proportion of tunic (morphology) and short-lived (longevity) trait categories and a higher proportion planktonic larval recruiters (larval development mode) compared to some, but not all, habitats. When categorised by k-means clusters, the infaunal assemblages displayed a greater number of trait differences between habitats compared to that based on EUNIS habitats; assemblages of Clusters 1, 3 and 4 showed the greatest difference across a larger range of traits. The greater between-habitat trait composition differences observed for the cluster approach relative to the EUNIS habitat method of habitat classification implies that the former habitat classification method is more suitable for encapsulating the functional variability of infaunal assemblages. That is, the cluster habitats comprise assemblages that are functionally more discrete from each other compared to EUNIS habitats. It follows, therefore, that assessing the functional variability of infaunal assemblages, and its response to natural or anthropogenic drivers, is more appropriately studied at the scale of environmentally-derived habitats compared to EUNIS habitats (at least at EUNIS level 4).

It is important to determine whether these trait composition differences lead to functional differences; unfortunately, without empirical or observational data, or measurements regarding functional properties, we are unable to draw parallel links as to the functional implications of the trait differences we have observed between habitats. The results obtained in the present study will subsequently be used in conjunction with further work to be conducted under WP3 and WP4 to address this knowledge gap (see Section 5).

4.2 Effects of fishing on trait composition of benthic assemblages

4.2.1 The overall effect of fishing activity on biological traits compostion

A number of studies have been conducted to assess the effects of habitat disturbance by fishing on benthic assemblage trait composition (e.g. Bremner *et al*., 2005; Tillin *et al*., 2006; de Juan *et al*., 2007; Kenchington *et* *al*., 2007; Fleddum *et al*., 2013). These studies have been conducted across a variety of habitats and regions (although generally shallow water); encompass a range of fishing intensities and different spatial and/or temporal scales; vary in their estimation methods of fishing pressure and, moreover, greatly vary with respect to survey designs and assessment approaches (Thrush and Dayton, 2002). The selection of the traits used for traits analysis, for example, can have large implications for the resulting outcomes of a study (Bremner, 2008). Furthermore, fishing activities are likely to markedly vary with respect to gear type between studies, further confounding any inter-study comparability. The larger number of stations across a wide range of habitats and spatial scales included in the present study minimises, to a certain extent, the problems otherwise associated with inter-study comparisons. Our data revealed that biological trait composition response to fishing was habitat-dependent. Although some traits respond in a similar way to fishing across a range of habitats, others respond in a habitat-specific manner. The explicit finding that different traits display different responses to fishing across different habitats implies that trait responses observed by different studies must always be placed into context with the habitat under investigation. Often, however, habitat information is either not given, or the method used to determine habitat characteristics varies between studies; both of these make it difficult to assess habitat-specificity of trait responses to fishing impacts from published studies.

Small-bodied organisms, commonly found to be favoured by fishing (Bremner et al., 2005; Atkinson et al., 2011), displayed a significantly positive correlation with FP in some habitats studied here (e.g. A5.13, infralittoral coarse sediment; A5.25, circalittoral fine sand) whilst the numerical proportion of the smallest size class (i.e. < 10 mm) showed a significantly negative correlation with FP in A5.26 (circalittoral muddy sand). A number of other trait categories (e.g. suspension- and sub-surface deposit feeders) similarly displayed an inconsistent fishing response across traits. However, trait categories of some traits (e.g. living habitat and morphology) tended to show a more consistent response to fishing across habitats in the present study, for both infauna and epifauna. Attached, stalked and epiphytic traits were commonly found to show a significant negative correlation with total FP across habitats.

While the response of many of the various trait categories differed between habitats, this study found, that for infaunal and epifaunal assemblages, habitats varied in the magnitude (as defined by the number of trait categories having a significant correlation with FP) of their responses to FP. While the assemblages of some habitats (e.g., A5.45 - deep circalittoral mixed sediments and those of Clusters 2, 3 and 5 for infauna; A4.2 - Atlantic and Mediterranean moderate energy circalittoral rock and A5.4 - sublittoral mixed sediments for epifauna) showed either an absence or very little trait variation in response to fishing, others responded by significant variations in the percent composition of a relatively high number of trait categories. It is possible that this observation may result from differences in estimated FP between the habitats as opposed to inherent differences in their response to fishing. A5.45, for example, together with habitat clusters 2, 3 and 5, may be regarded, in general, as being exposed to a lower fishing pressure than other habitats (Figure 6a and b). Similarly, for the epifauna, the relatively small trait response of the assemblages of A4.2 may arguably be associated with the somewhat lower FP values estimated for that habitat.

The results obtained in the present study support the observations of others regarding the functional effects of fishing, but these functional impacts are likely to be habitat dependant. For example, it has been observed that increased fishing leads to a decrease in biodiversity, reduced benthic-pelagic coupling of nutrients and carbon flow while, in some cases, also yielding an increased secondary production due to a reduction in long-lived, slow-growing organisms and an enhancement of the proportion of smaller, fast-growing individuals. We observe that fishing leads to a reduction in the numerical proportion of sessile, stalked (or other taxa with a vertical morphology) and epiphytical invdividuals across a number of habitats; traits which may be regarded as being associated with increased diversity. Similarly, bed-modifers and reef-formers showed negative correlations with FP in a number of habitats such as A5.13, A5.23, A5.25 and A5.35. As previously mentioned, however, it is not possible to unequivically imply functional change based on variations in trait composition in the absence of empirical data.

We reveal that, under no- or low-fished conditions, trait composition does not vary significantly between most habitats, yet, under increasing fishing pressure, various traits displayed a range of relationships with total FP across habitats. This habitat- and trait-specific response implies that it is possible that variations in assemblage trait compositions are greater across fishing gradients than they naturally would be across different habitats in the absence of fishing. It follows, then, that the functioning of the ecosystem may be influenced by fishing, but that the nature of this response is very complex (e.g. regional scales, habitat and trait differences). This finding has potential significance for studies aiming to understand the relationships between benthic function and environmental variability. For example, many studies have been conducted to assess the spatial changes in trait composition along environmental gradients or over large spatial scales which incorporate a range of habitats; our results imply that fishing intensity differences need to be controlled/accounted for in order to truly identify the relationships between traits and environmental variability.

4.2.2 Effects of gear type

It is, however, possible that the differences in trait responses we observe between habitats may not only reflect inherent differences in the responses of assemblages to total fishing pressure, but also varying responses due to various gear types. We observed that, for many habitats, FP was governed predominantly by one gear type, with the dominant gear type varying between habitats. A number of authors have emphasized the need to consider the interaction between fishing gears and the observed biological responses (e.g. Kaiser *et al.*, 2006); indeed, the nature of the physical effect on the bed differs markedly between the various fishing gear types. We observed that fishing activity at the infaunal stations possessing coarse or mixed sediments (A5.13 - infralittoral coarse sediment; A5.14 - circalittoral coarse sediment; A5.15 - deep circalittoral coarse sediment; A5.43 - infralittoral mixed sediment; and the shallow, gravelly sand habitats experiencing strong bottom flows - Cluster 1) was mainly dominated by demersal seine nets, while fishing in relatively fine-sediments habitats (e.g., A5.24 - infralittoral muddy sand; A5.26 - circalittoral muddy sand; A5.27 - deep circalittoral sand; A5.37 - deep circalittoral sandy mud; and the deep, muddy sand and slightly sandy mud bottoms of the Norwegian shelf - Clusters 2 and 3) was mainly by demersal otter trawls. Although the lower EUNIS level classification used makes it more difficult to ascertain, a similar association between these two predominant trawl types with bed substrate was discernible for the epifaunal stations. This relationship between gear type and habitat type prevents us from easily assessing whether the differences in the responses we observed between habitats (Section 4.2.1) were largely due to gear type variations or inherent properties of the assemblages. However, five of the eight habitat Cluster groups (i.e. Clusters 2, 3, 4, 5 and 7) were shown to display similar trawling characteristics, trawling within each being dominated by otter trawling (Figure 8). The assemblages of these five cluster habitats all displayed a similar trait response (Figure 16), i.e., they generally displayed a reduced trait response relative to the assemblages of Clusters 1, 6 and 8. Meanwhile, the infaunal assemblages of Clusters 1, 6 and 8 all showed different trait responses with total FP, and experienced greater trawling from beam trawls and seine trawls (Clusters 1 and 6). This association between gear types and trait responses may imply that the habitat differences we observe may result from gear differences as opposed to dissimilarities in the inherent responses of the assemblages. There is further evidence to support this when the infaunal stations were categorised according to EUNIS. A5.25 (circalittoral fine sand) and A5.13 (infralittoral coarse sediment) showed comparable trait responses (Figure 14) and both experienced relatively higher seine trawling and less otter trawling than other habitats. A5.23 (infralittoral fine sand) and A5.15 (deep circalittoral coarse sediment)), however, displayed similar trawling characteristics (generally comparable proportions of beam, seine and otter trawling) whilst exhibiting divergent trait responses to total FP. Our data indicate gear type may also be influential in affecting the traits of epifaunal invertebrates responses to trawling, more so than habitat type. Trait responses of A5.3 (sublittoral mud) and U_DCS (deep circalittoral seabed) to trawling, for example, were similar (Group A) and also possessed similar trawling profiles across the various gear types. Furthermore, the traits of areas U (unclassified) and A5.4 (sublittoral mixed sediments), both being trawled predominantly by otter trawls but also significantly (25-50%) by seine trawling, responded in a similar manner to total FP. The present data will be used further within Benthis to elucidate the relationships between gear type and impacts on benthic function. This will be conducted using a range of approaches, including a more detailed appraisal of the depth and type of physical impact of each gear type on the bed and how this varies between substrate type, together with a number of studies focussing on the acute biological and biogeochemical impacts of trawl passes on the seabed. The data presented here will be used alongside the results obtained from these various approaches to allow improved insights regarding the functional impacts of fishing on the seabed.

4.3 Effect of choice of habitat classification

When attempting to understand the processes driving ecological functioning, or the response of ecological components (e.g. macrofauna) to anthropogenic pressure, it is fundamentally important to determine the most appropriate spatial scale upon which to study, or how to most suitably delineate management boundaries. In the present study, the infaunal stations were assigned into habitats using two approaches; a

EUNIS approach and a k-means clustering approach based on a number of environmental variables. For the EUNIS approach, infaunal stations were categorised according to a pre-determined set of possible habitat categories (at EUNIS level 4) such as A5.13, A5.14, A5.15, etc. In contrast, the k-means approach involved assigning stations into habitat types that resulted from a clustering process, based on data describing the environmental characteristics of the stations. Comparing the results presented in Sections 3.2 and 3.3 allowed an evaluation of the most suitable approach for assessing trait composition variability (Section 3.2) and the potential functional impacts of fishing (Section 3.3). Direct comparisons may not be considered appropriate due to differences in the numbers of habitats categorised by the two methods (i.e., 13 EUNIS habitats compared to 8 cluster group habitats). There were no notable differences in the degree of assemblage trait compositional differences between EUNIS habitats, compared to that when stations were grouped according to k-means clustering, partly as the underlying outcome was that of a large amount of within-habitat variation relative to between-habitat variation (Section 3.2). However, one may argue that although between habitat differences in assemblage trait composition were somewhat more apparent using the clustering approach, there is no formal method with which to test this. For example, four traits showed marked between-habitat difference using the EUNIS approach, while seven traits displayed notable differences between habitats based on the k-means clustering method. Similarly, these two methods of habitat classification revealed differences in the way trait composition is affected by increased total fishing activity between habitats (Section 3.3). We must remember that the allocation of each infaunal station to a EUNIS habitat in the present study was based on observed granulometric data and, thus, the EUNIS habitat was arguably a better depiction compared to that as predicted using EUSeaMap. In this respect, potential differences between the two approaches were reduced.

These results do not necessarily imply that trait composition, nor its response to fishing, is clearly better assessed according to one approach than the other. It does, however, indicate that different approaches can lead to different outcomes and, thus, careful consideration is needed when allocating sampling observations into distinct habitats so as to control for the effects of environmental factors during assessments of the impacts of fishing on biological traits.

4.4 Limitations and constraints

There are a number of logistical, scientific and methodological aspects of the work conducted here which have implications for the outcomes observed. These aspects must be considered when interpreting the data, and, in addition, have implications for our ability to address the ecological questions being set. These aspects are summarised below:

- Many of the regions included in the present study have a long history of fishing, yet our estimations of FP were based on data limited to 2010-2012 (incl.). Thus, we have to make the assumption that the data used to estimate FP for our stations apply to fishing activities over the period from which the faunal data were acquired, generally from 2000 onwards (depending on the data source). Hiddink *et* *al*. (2006) found a strong correlation between the VMS data used in their study (from 2000-2002) in the North Sea with older over-flight data, indicating that spatial patterns of fishing activity in that region, at least, were relatively stable. Moreover, however, we cannot account for the spatial variation in fishing activity over much longer timescales, during the previous century when, arguably, most of the more fundamental habitat alterations affecting benthic may have occurred.

- The fishing pressure estimates provided by DTU_Aqua under the auspices of WP2 do not provide full coverage of the total fishing effort with mobile, bottom contacting gears of the case study areas. Calculation of the fishing pressure are based on VMS data and, as this equipment is only mandatory for vessels of at least 12 metres in length, all effort with smaller vessels is overlooked. It is likely that this is predominantly an issue in coastal waters, as small vessels only rarely fish further offshore. Additionally, not all countries with commercial fishing fleets in the case-study areas completed the required workflow under WP2, and, thus, the FP estimates used during this study do not include fishing activities by these countries.
- Trait composition was derived based on abundances as opposed to biomass for this study. This selection was imposed by a logistical constraint resulting from only a partial availability of biomass data for our sampled stations. Published studies using BTA on marine benthic assemblages have used either abundance or biomass during trait composition derivation and, often, there is little or no justification for the selection. Bolam and Eggleton (2014) demonstrated that the outcomes of traits analyses are, indeed, affected by the choice of weighting used during traits analysis and, thus, we must bear in mind the implications of our abundance-based, as opposed to biomass-based, traits analysis when making inferences regarding the implications of the findings to fisheries management.
- The present study was based on data from a number of participants and includes data from a range of habitat types across European shelf seas. We aimed to maximise the amount of relevant data included in the current analysis so as to enhance our ability to estimate trait composition of each habitat. We acknowledge that the relative spatial extents of seabed each habitat occupies varies widely and we have made no attempt to stratify the number of our stations in accordance with these relative differences. This is largely a constraint imposed by a lack of available data and it is likely that some habitats are represented by a disproportionate number of stations, relative to their geographical coverage.

5. FURTHER WORK AND UPTAKE OF RESULTS WITHIN BENTHIS

The analyses undertaken and the results presented here were conducted to meet the requirements of a deliverable (D3.1.1), under the auspices of Benthis WP3. While the work detailed has involved the input from a number of source participants within Benthis (i.e., the data contributors), the outcomes will be reviewed by other participants within Benthis, and the relevant information resulting from this review will be used to revise the report content. It might be deemed necessary, for example, to undertake further analysis regarding certain geographical regions, certain habitats or conduct a specific piece of additional analysis to understand the effects of certain gear types on the trait composition of a range or of a particular habitat or assemblage type. Any such further development will be governed by the conclusions of subsequent discussions between the entire Benthis project team.

Within WP3, work is currently underway to quantify seabed function with respect to productivity and value (as a source of food) to commercially important fish species and to relate this to the sensitivity, resilience and resistance properties of macrobenthic assemblages. This involves an assessment of the traits composition of the benthic prey of fish using fish gut content analysis, and the trends in the preys' trait composition will then be integrated with those of the habitats where the fish species feed. The habitat-trait composition analysis undertaken herein will be used as part of this assessment. It is envisaged that this trait-based, as opposed to structure-based, approach to understanding the energetic or trophic importance of benthic assemblages will overcome some of the species-specific variability hitherto associated with stomach contents analysis data and, therefore, result in a more robust methods of decoupling the functional predator-prey relationships associated within specific seabed habitat types across large spatial scales.

6. ACKNOWLEDGEMENTS

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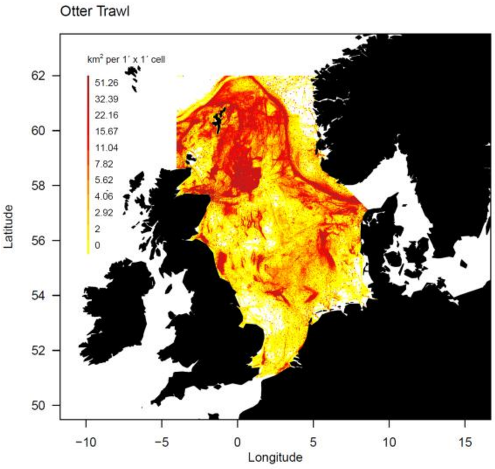
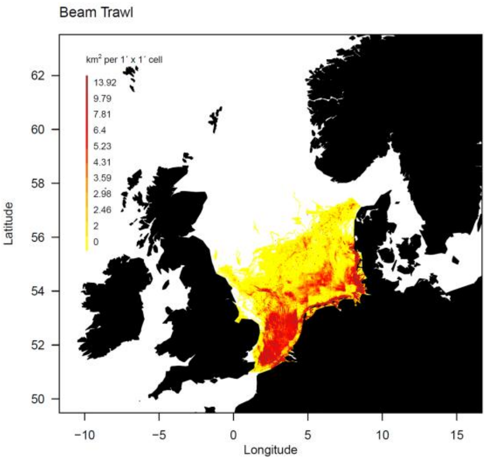
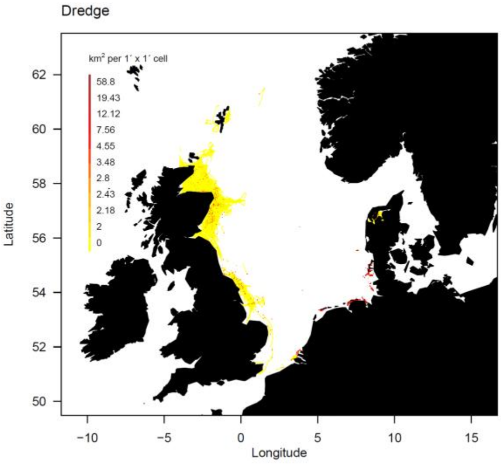
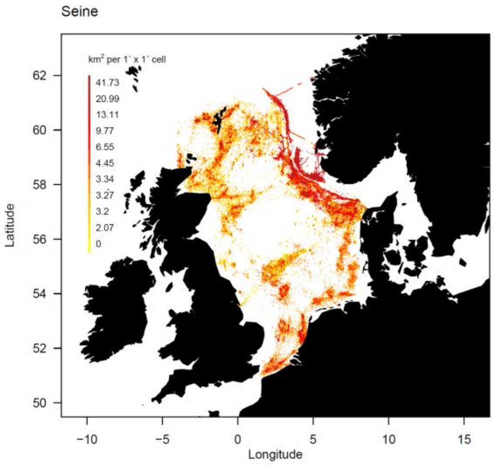
APPENDIX 1: *Fishing pressure intensities expressed as total swept area from 2010-2012 in grid cells of 1x1 minutes (or 1.9 km*^{2} *at 56*^{o}*N) for four different gear groups: otter trawl, beam trawl, dredge and seine. Data from Norwegian, Swedish, Danish, German, Dutch, Belgian, English and Scottish vessels in the North Sea (only). Lower decile bounds are depicted in the legend. A swept area of 51 km*^{2} *means that the grid cell is swept 27 times in 3 years.*


Otter Trawl
km^2 per 1´ x 1´ cell
51.26
32.39
22.16
15.67
11.04
7.82
5.62
4.06
2.92
2
0
Latitude
62
60
58
56
54
52
50
Longitude
−10
−5
0
5
10
15

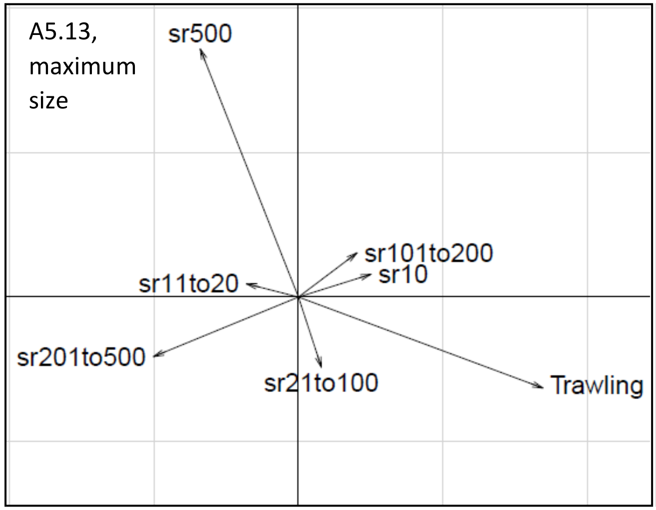

Beam Trawl
km^2 per 1´ x 1´ cell
13.92
9.79
7.81
6.4
5.23
4.31
3.59
2.98
2.46
2
0
Latitude
62
60
58
56
54
52
50
Longitude
−10
−5
0
5
10
15

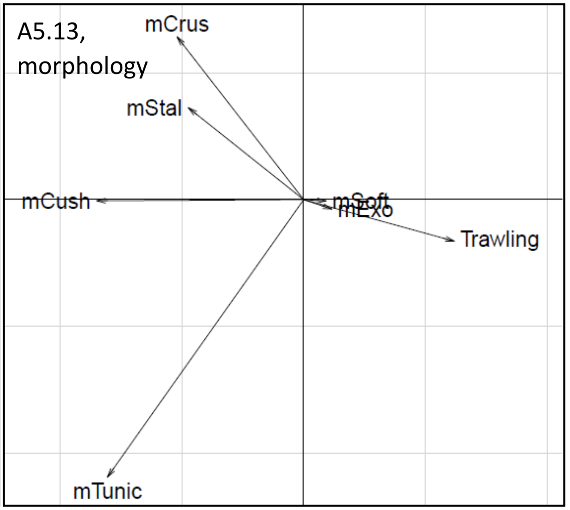

Dredge
km^2 per 1´ x 1´ cell
58.8
19.43
12.12
7.56
4.55
3.48
2.8
2.43
2.18
2
0
Latitude
62
60
58
56
54
52
50
Longitude
−10
−5
0
5
10
15

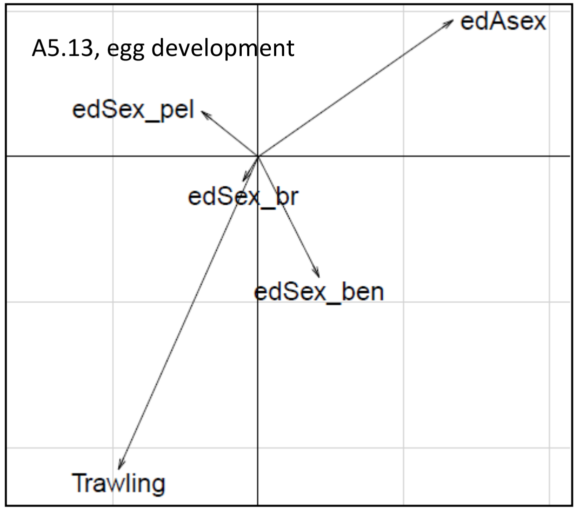

Seine
km^2 per 1´ x 1´ cell
41.73
20.99
13.11
9.77
6.55
4.45
3.34
3.27
3.2
2.07
0
Latitude
62
60
58
56
54
52
50
Longitude
−10
−5
0
5
10
15

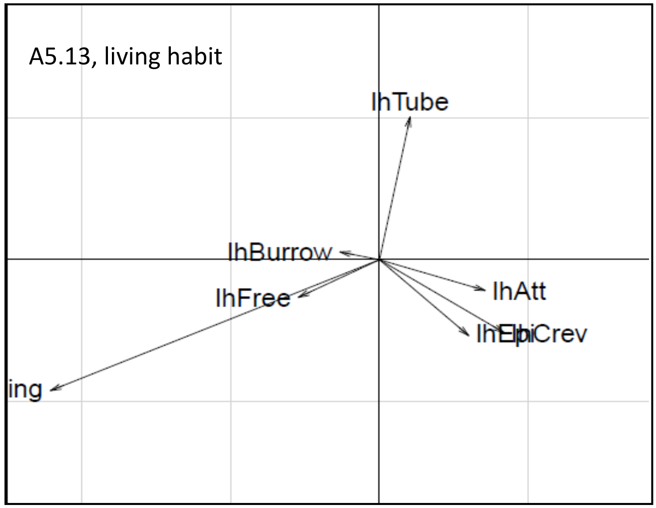
APPENDIX 2: FCA plots where a significant correlation between a trait category with FP was observed.

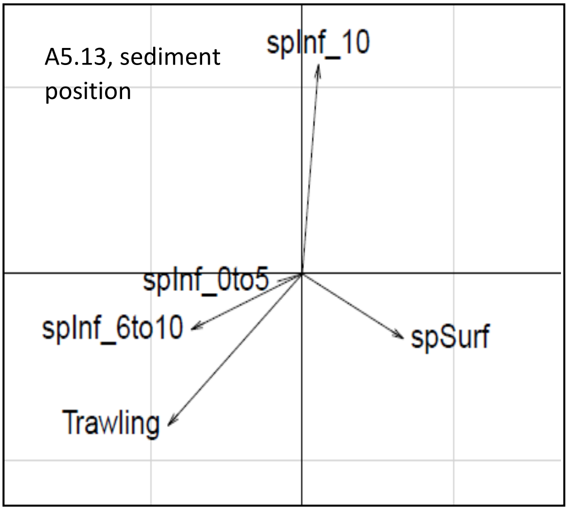
APPENDIX 2a: Infaunal stations by EUNIS habitat

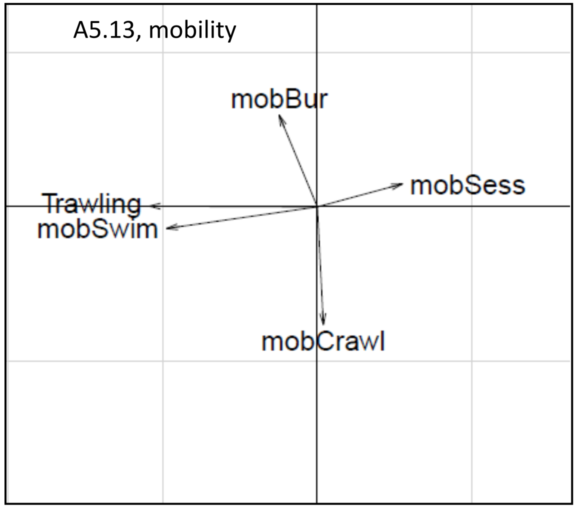

A5.13, maximum size
sr500
sr101to200
sr10
sr11to20
sr201to500
sr21to100
Trawling

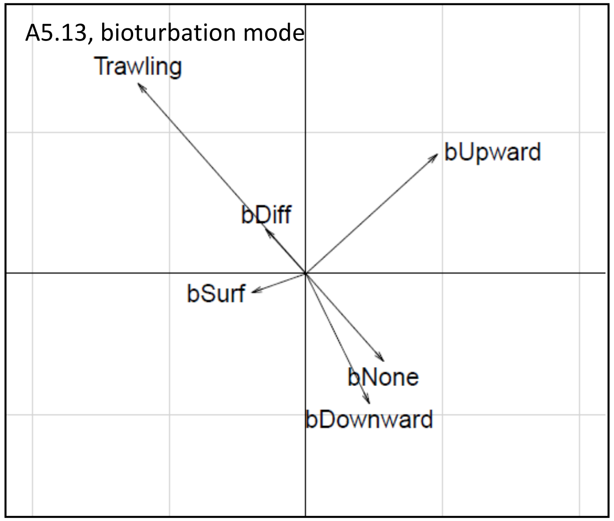

A5.13, morphology
mCrus
mStal
mCush
mSoft
mExo
Trawling
mTunic

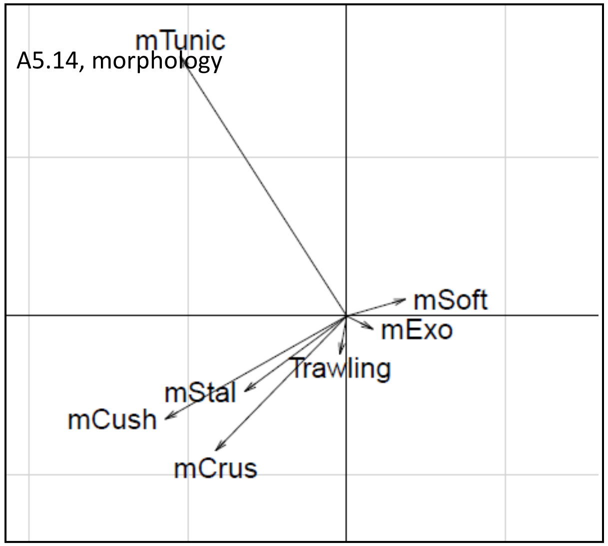

A5.13, egg development
edAsex
edSex_pel
edSex_br
edSex_ben
Trawling

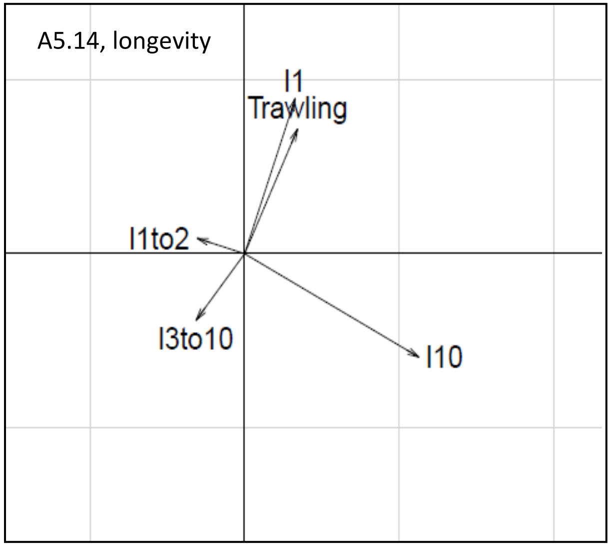

A5.13, living habit
lhTube
lhBurrow
lhFree
lhAtt
lhEpi
lhCrev
ing

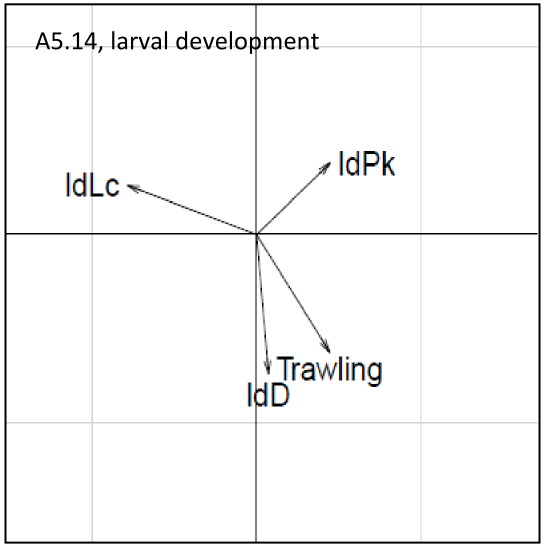

A5.13, sediment position
spInf_10
spInf_0to5
spInf_6to10
spSurf
Trawling

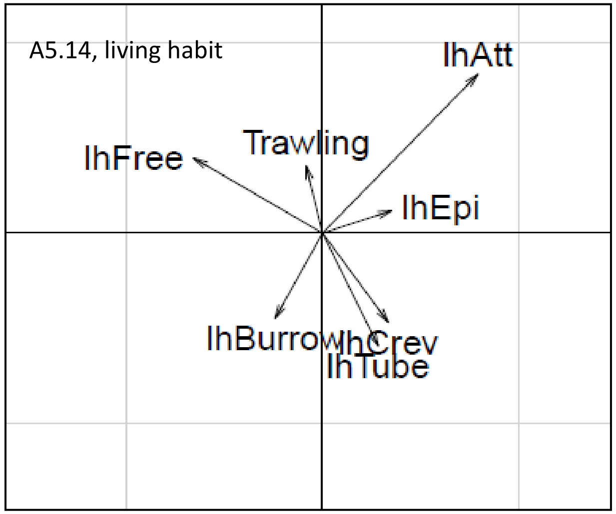

A5.13, mobility
mobBur
mobSess
Trawling
mobSwim
mobCrawl

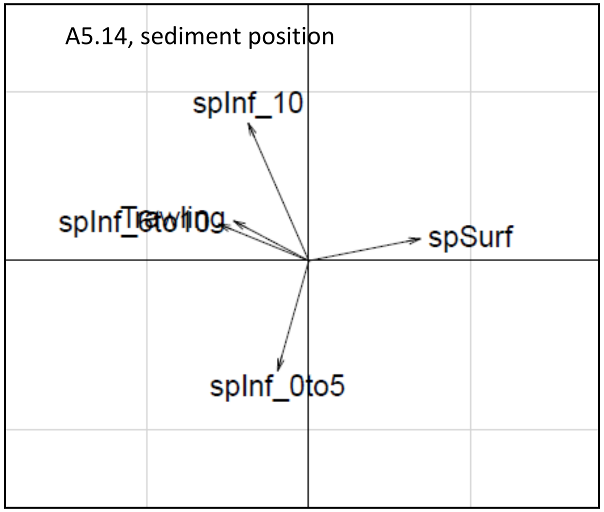

A5.13, bioturbation mode
Trawling
bUpward
bDiff
bSurf
bNone
bDownward

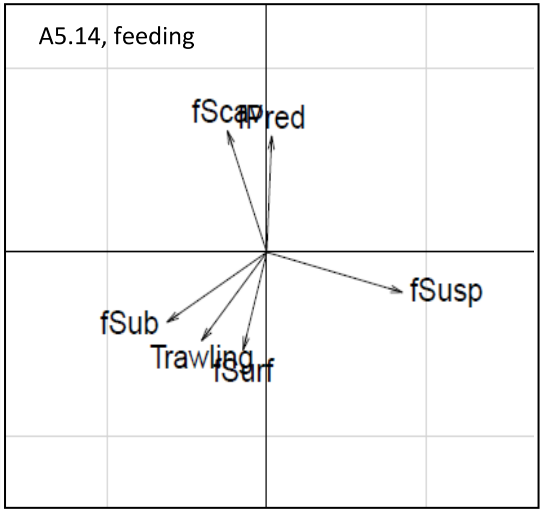

mTunic
A5.14, morphology
mSoft
mExo
Trawling
mStal
mCush
mCrus

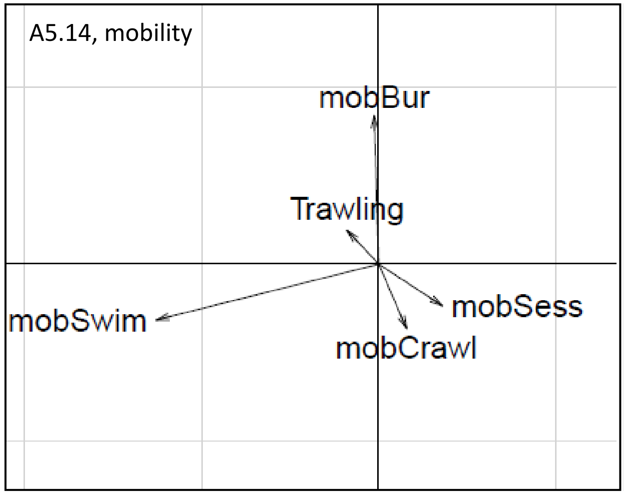

A5.14, longevity
l1
Trawling
l1to2
l3to10
l10

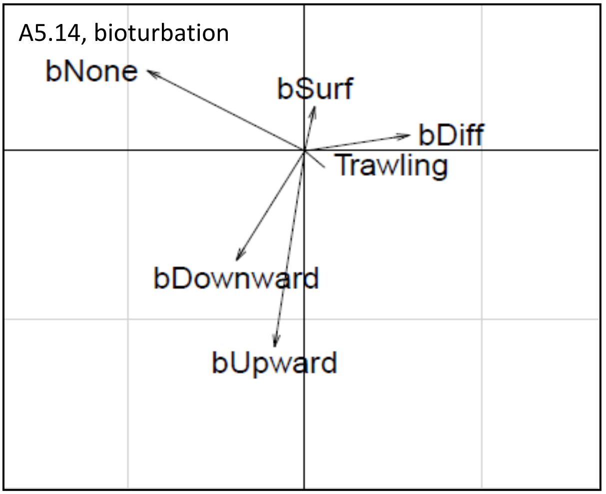

A5.14, larval development
ldPk
ldLc
Trawling
ldD

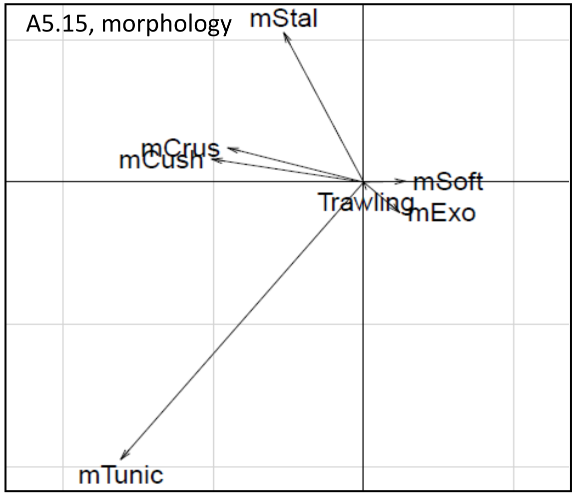

A5.14, living habit

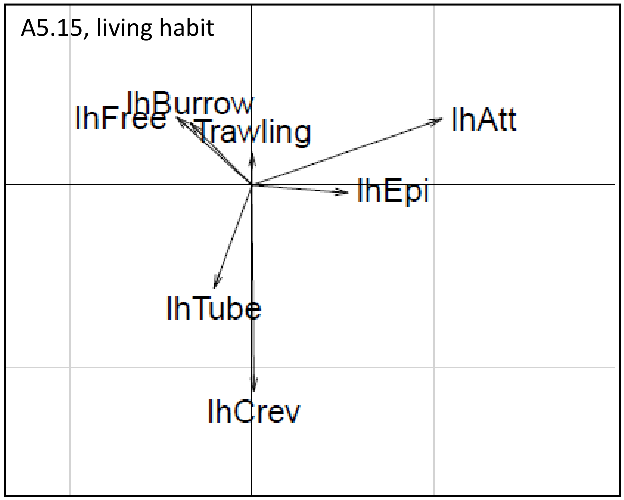

A5.14, sediment position

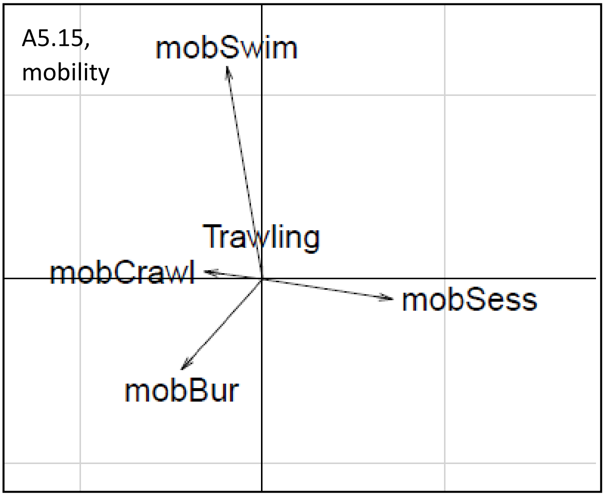

A5.14, feeding

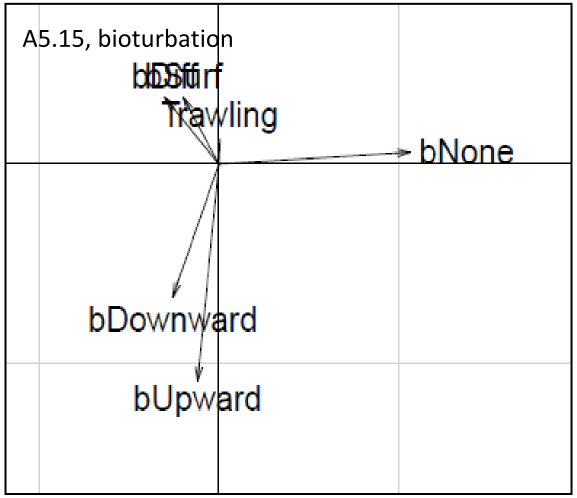

A5.14, mobility

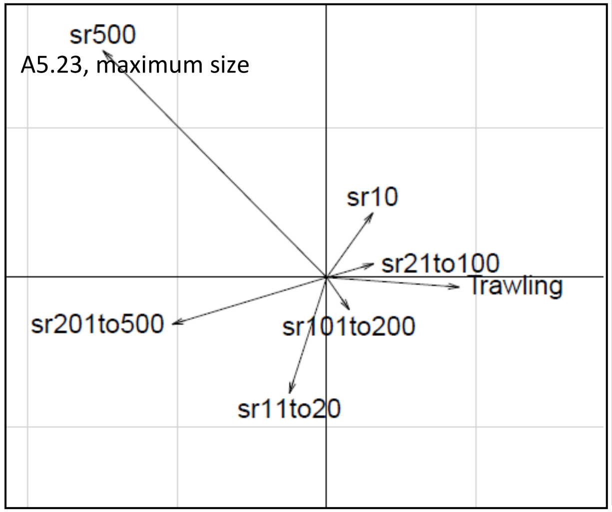

A5.14, bioturbation

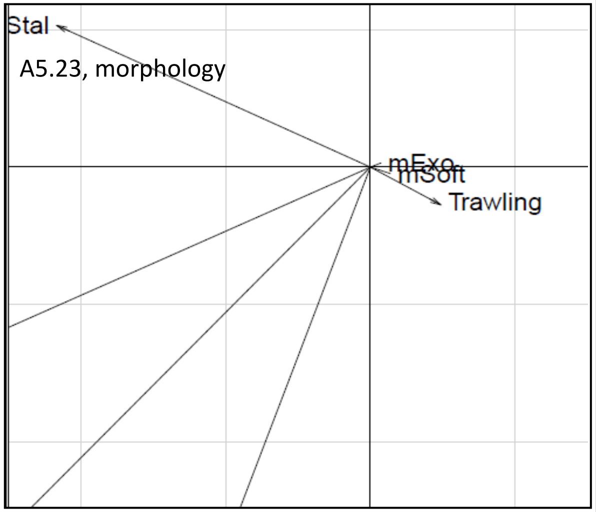

A5.15, morphology
mStal
mCrus
mCush
mSoft
Trawling
mExo
mTunic

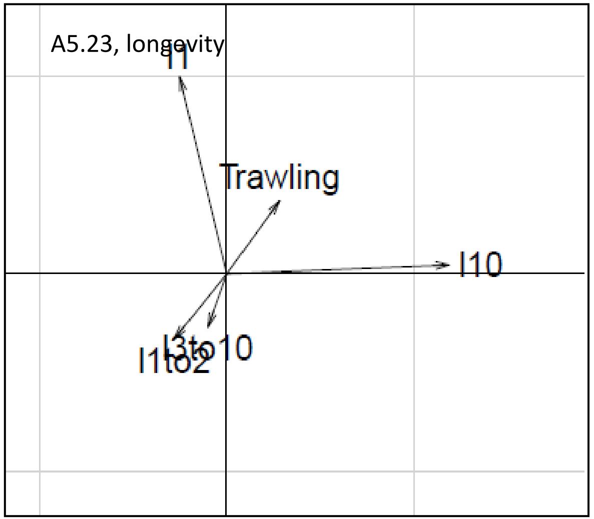

A5.15, living habit
lhFree
lhBurrow
Trawling
lhAtt
lhEpi
lhTube
lhCrev

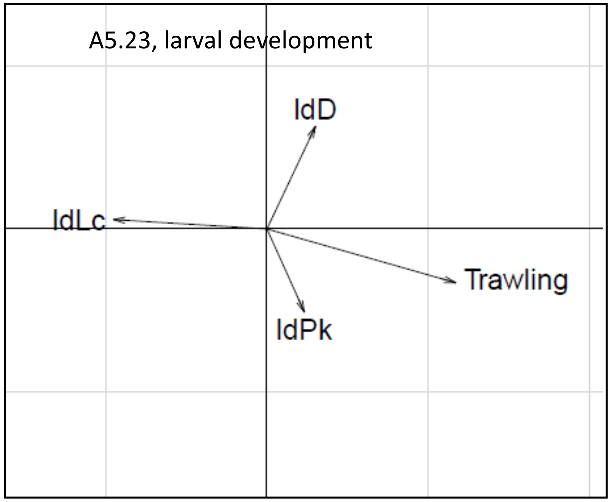

A5.15, mobility
mobSwim
Trawling
mobCrawl
mobSess
mobBur

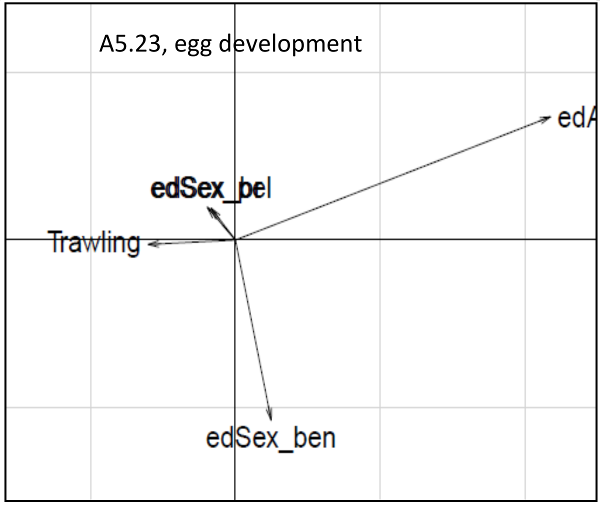

A5.15, bioturbation
bDiff
bSurf
Trawling
bNone
bDownward
bUpward

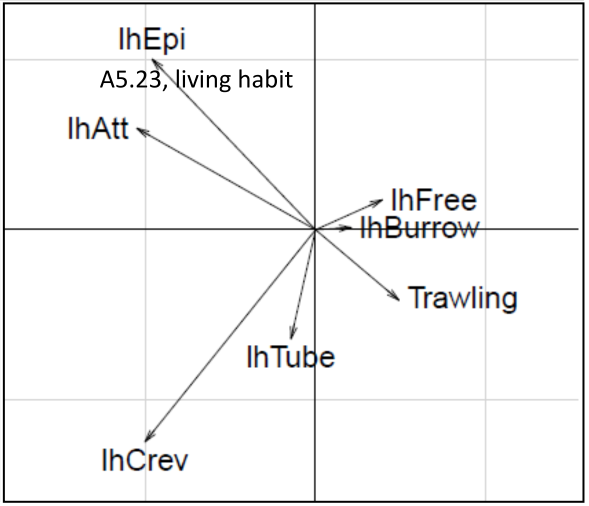

A5.23, maximum size
sr500
sr10
sr21to100
Trawling
sr201to500
sr101to200
sr11to20

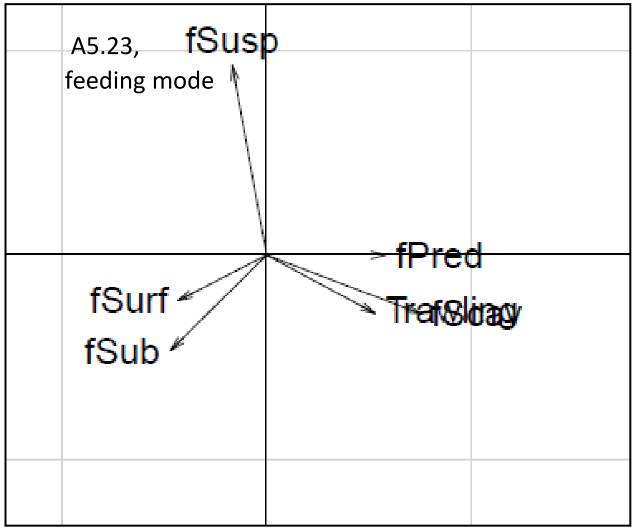

A5.23, morphology
Stal
mExo
mSoft
Trawling

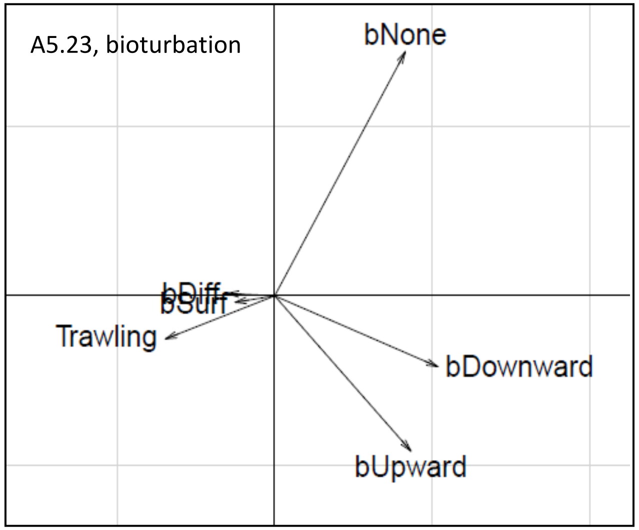

A5.23, longevity
l1
Trawling
l10
l1to2
l3to10

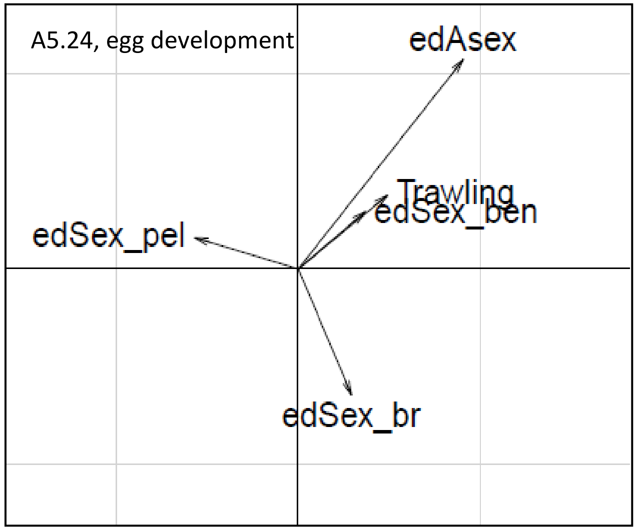

A5.23, larval development
ldD
ldLc
Trawling
ldPk

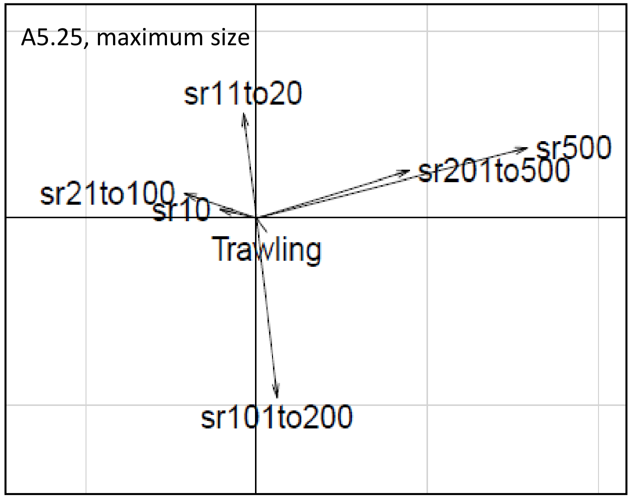

A5.23, egg development
ed
edSex_pel
Trawling
edSex_ben

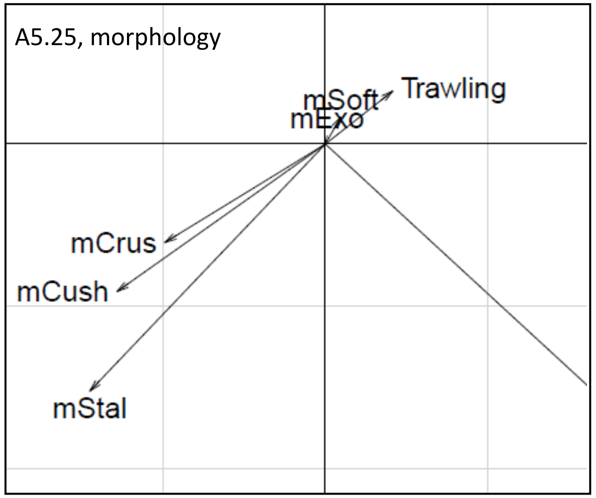

lhEpi
A5.23, living habit
lhAtt
lhFree
lhBurrow
Trawling
lhTube
lhCrev

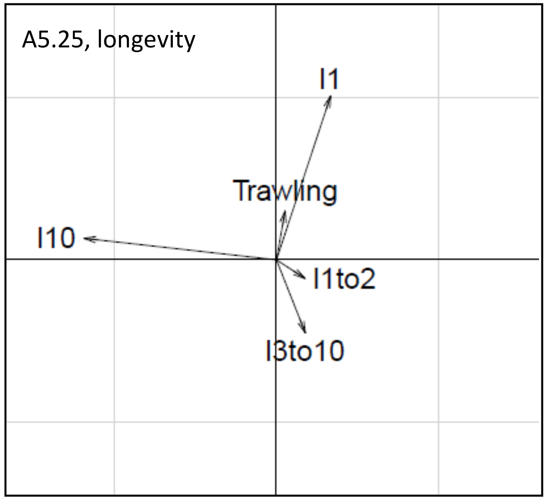

A5.23,
feeding mode
fSusp
fPred
fSurf
fSub
Trawling

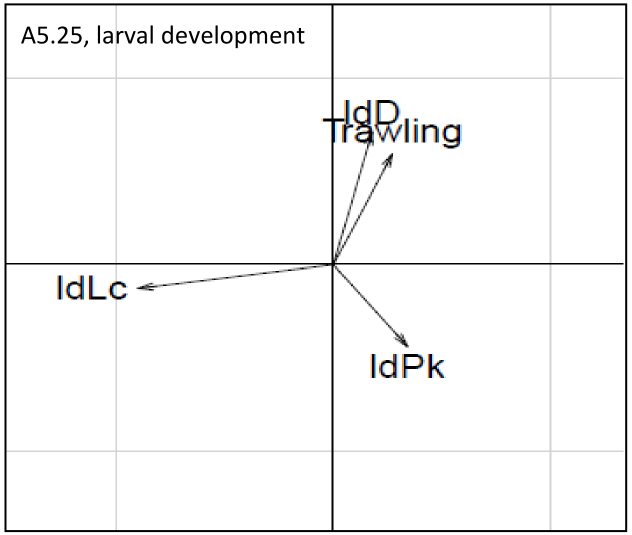

A5.23, bioturbation
bNone
bDiff
bSurf
Trawling
bDownward
bUpward

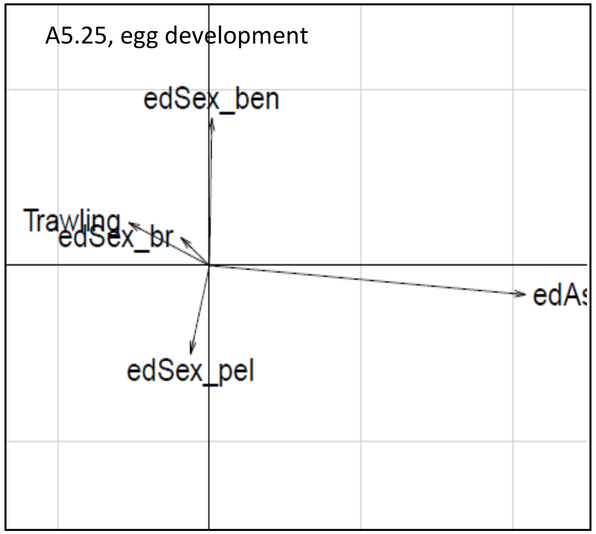

A5.24, egg development
edAsex
Trawling
edSex_ben
edSex_pel
edSex_br

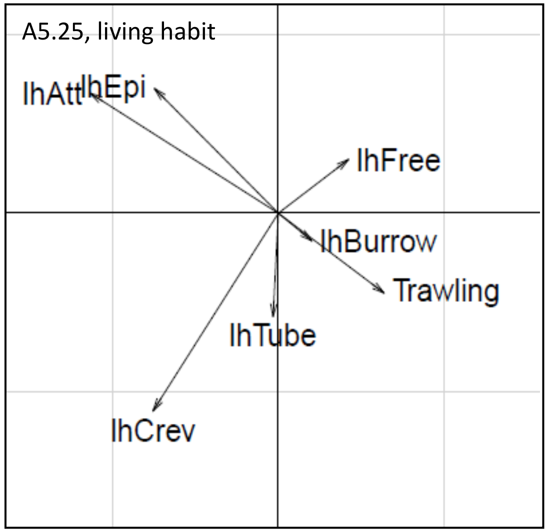

A5.25, maximum size
sr11to20
sr500
sr201to500
sr21to100
sr10
Trawling
sr101to200

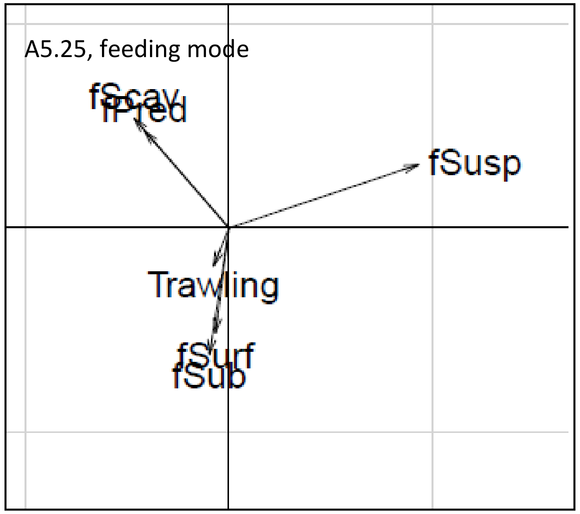

A5.25, morphology
mSoft
mExo
Trawling
mCrus
mCush
mStal

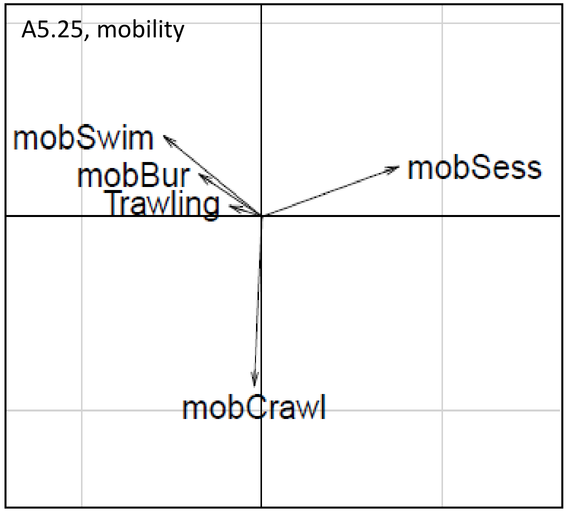

A5.25, longevity
l1
Trawling
l10
l1to2
l3to10

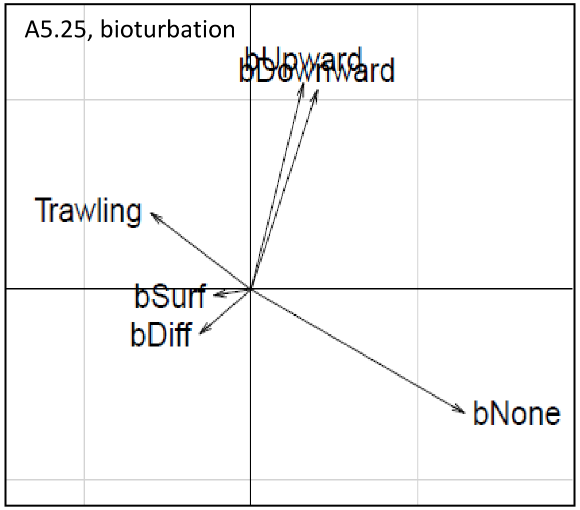

A5.25, larval development
ldD
Trawling
ldLc
ldPk

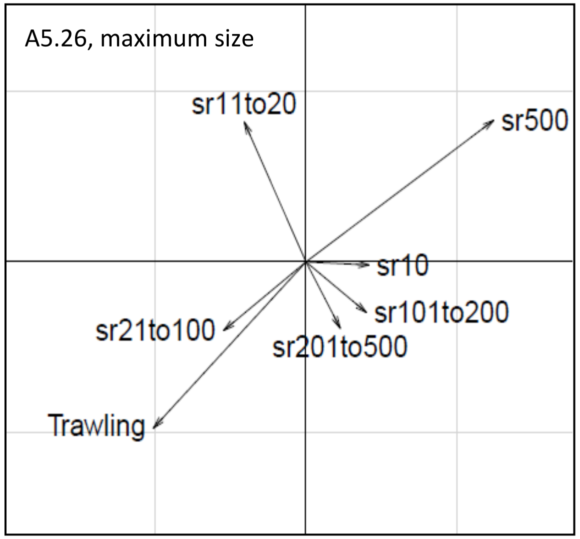

A5.25, egg development
edSex_ben
Trawling
edSex_br
edA
edSex_pel

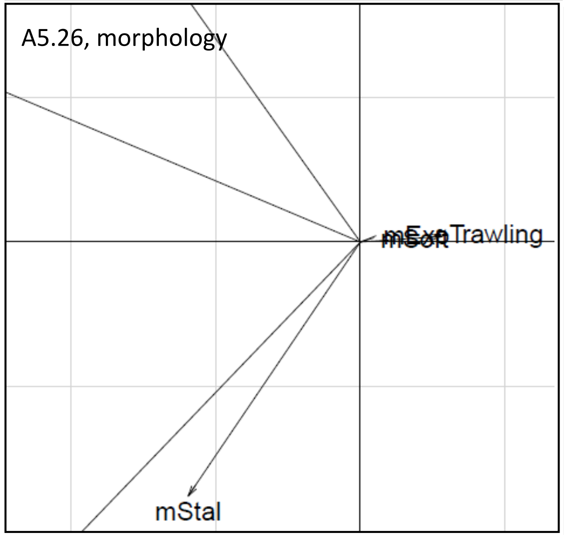

A5.25, living habit
lhAtt
lhEpi
lhFree
lhBurrow
Trawling
lhTube
lhCrev

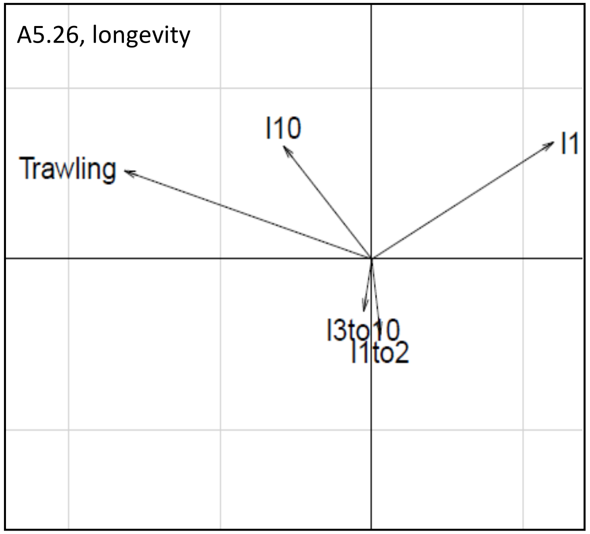

A5.25, feeding mode
fScav
fPred
fSusp
Trawling
fSurf
fSub

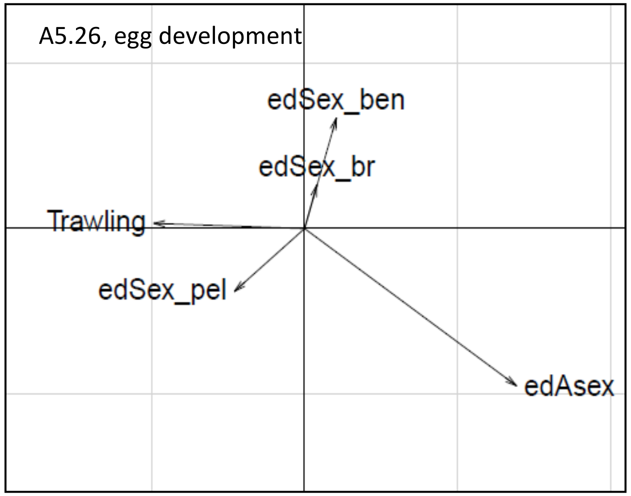

A5.25, mobility
mobSwim
mobBur
Trawling
mobSess
mobCrawl

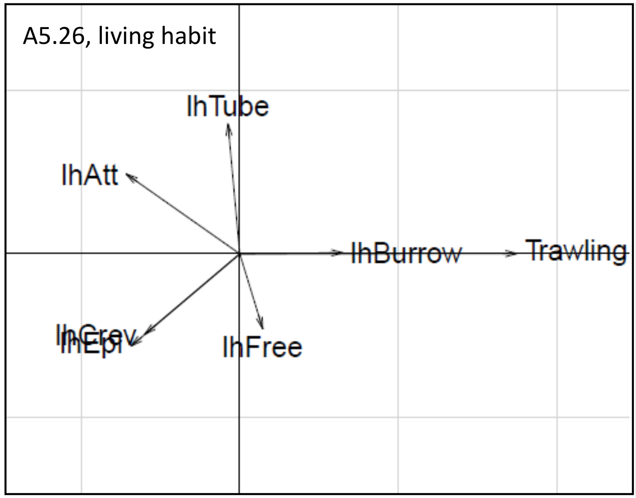

A5.25, bioturbation
bUpward
bDownward
Trawling
bSurf
bDiff
bNone

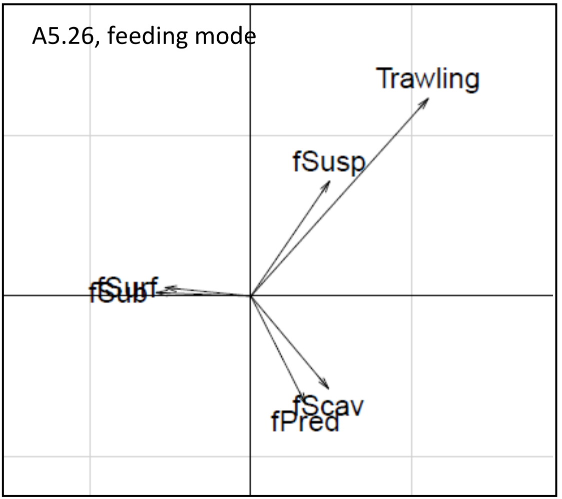

A5.26, maximum size
sr11to20
sr500
sr10
sr101to200
sr21to100
sr201to500
Trawling

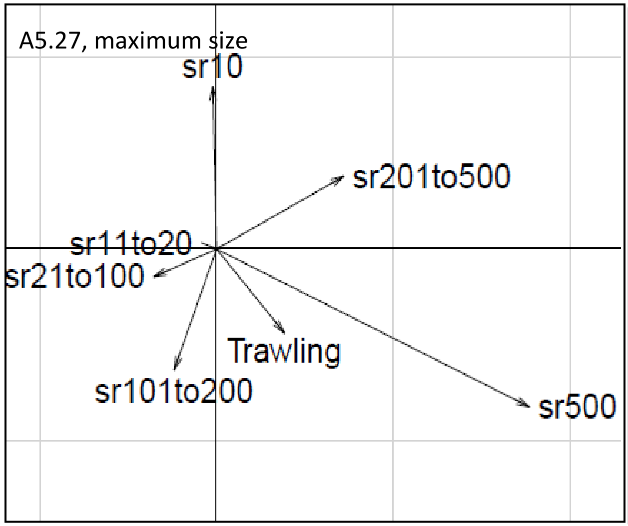

A5.26, morphology
mExp
mSoft
Trawling
mStal

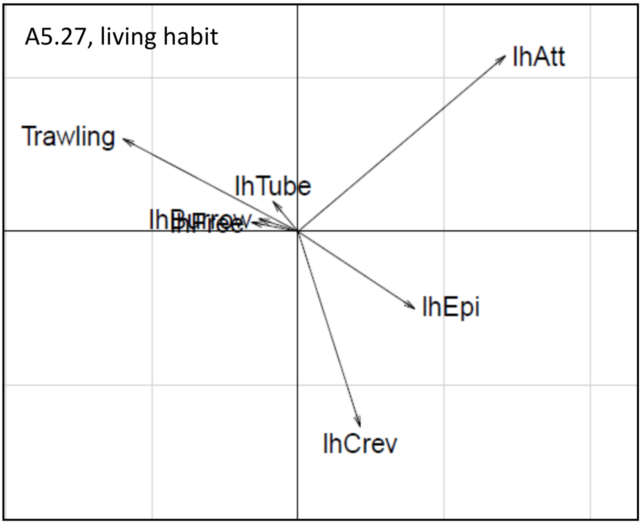

A5.26, longevity
l10
l1
Trawling
l3to10
l1to2

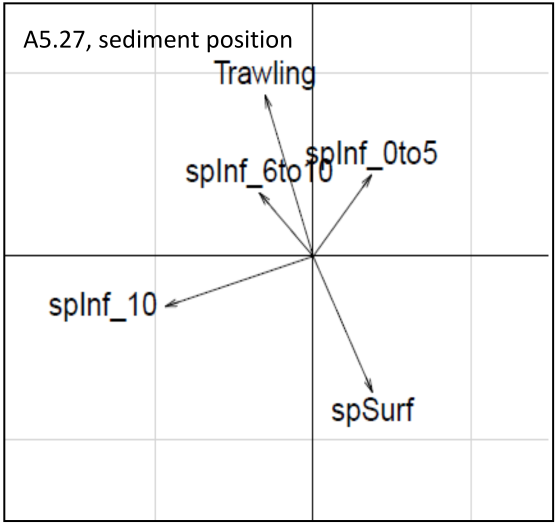

A5.26, egg development

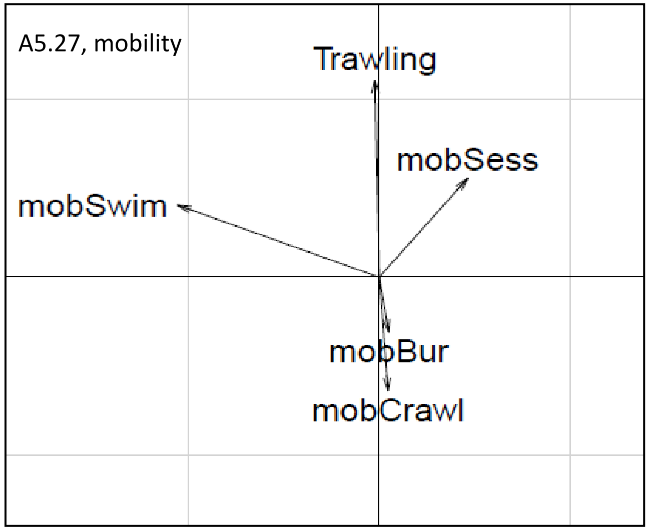

A5.26, living habit

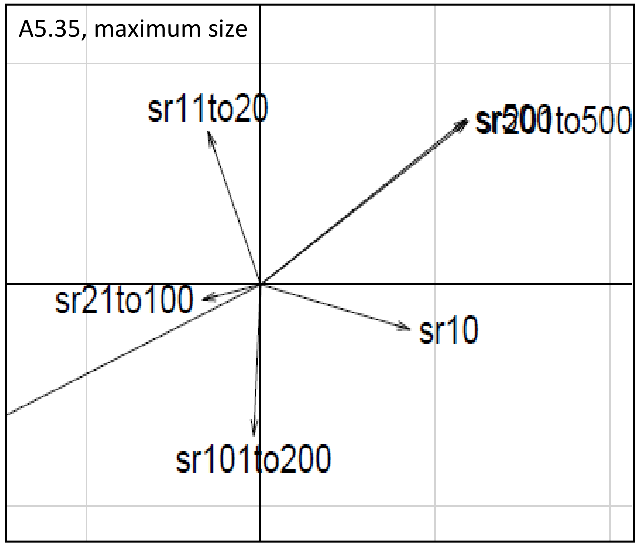

A5.26, feeding mode

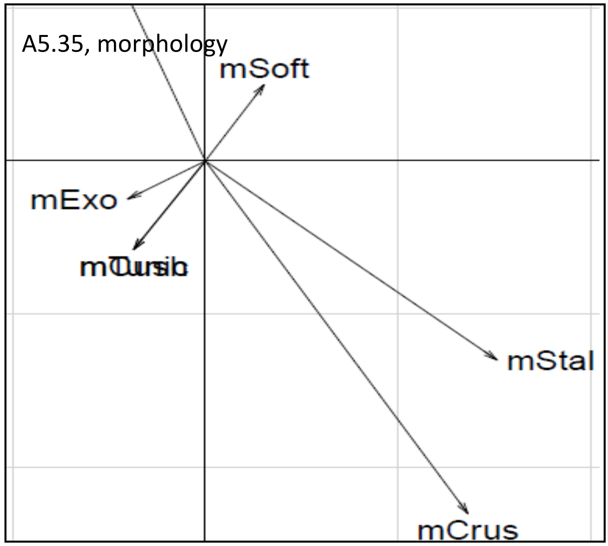

A5.27, maximum size

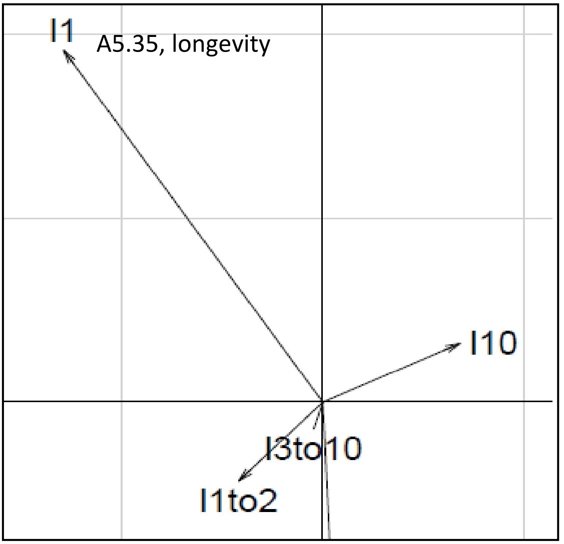

A5.27, living habit

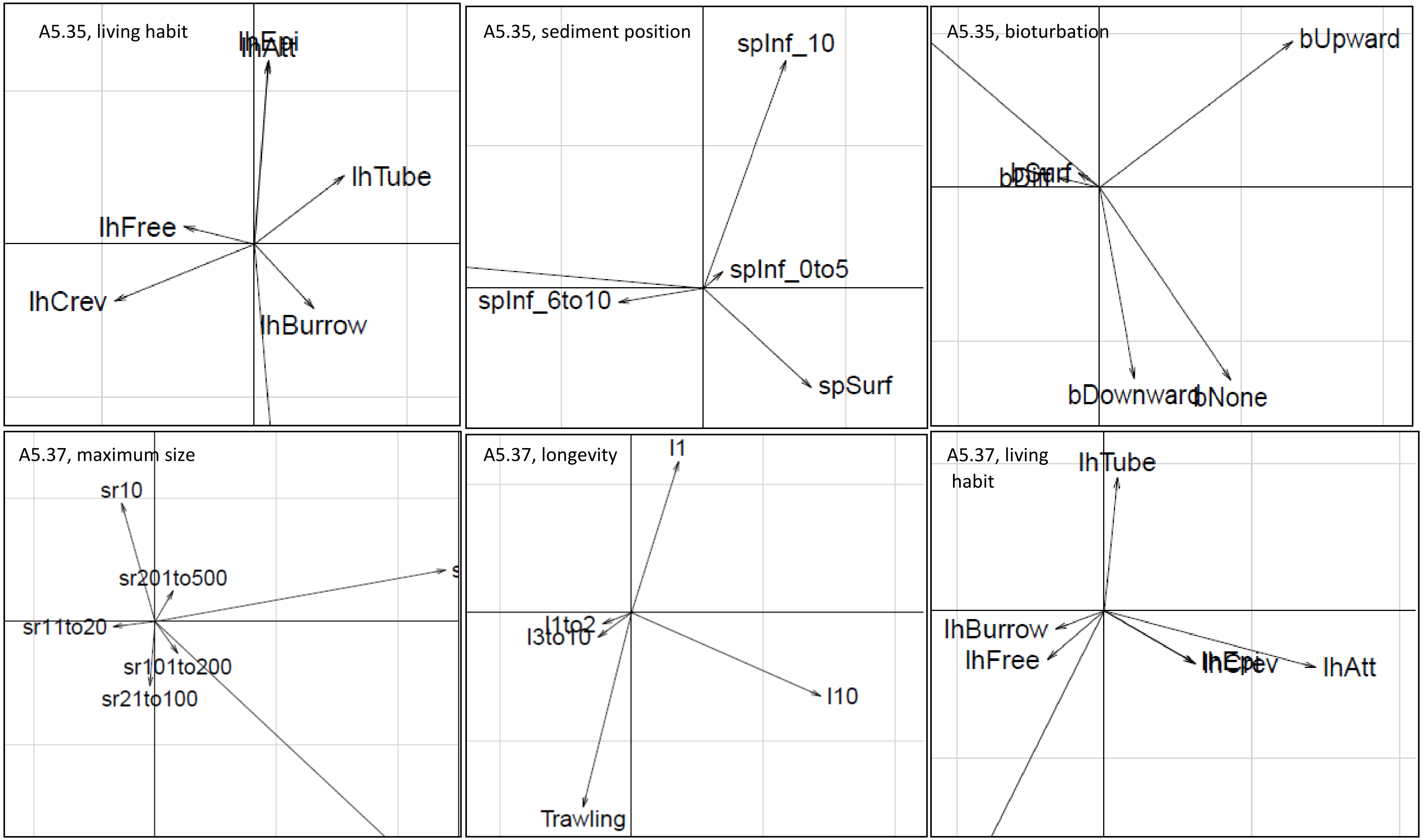

A5.27, sediment position

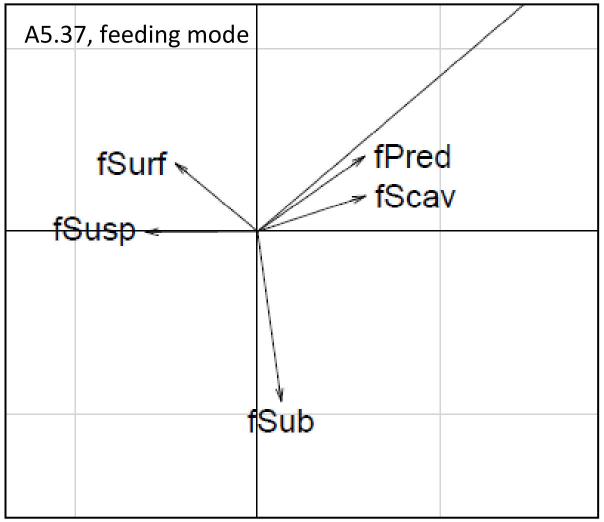

A5.27, mobility

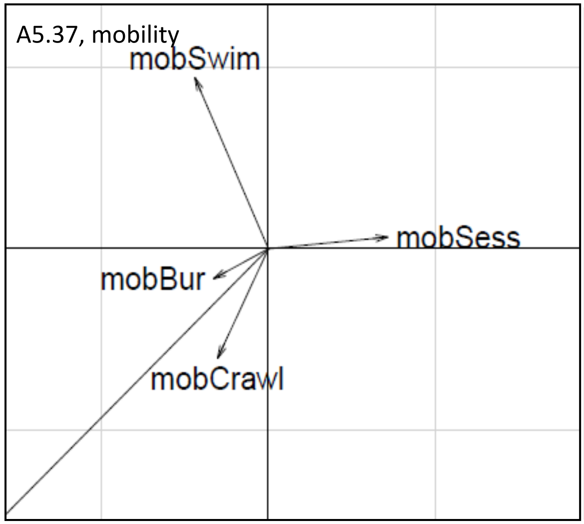

A5.35, maximum size

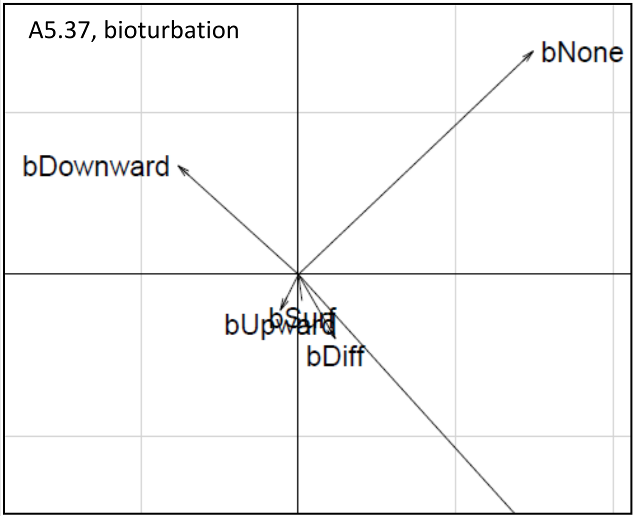

A5.35, morphology

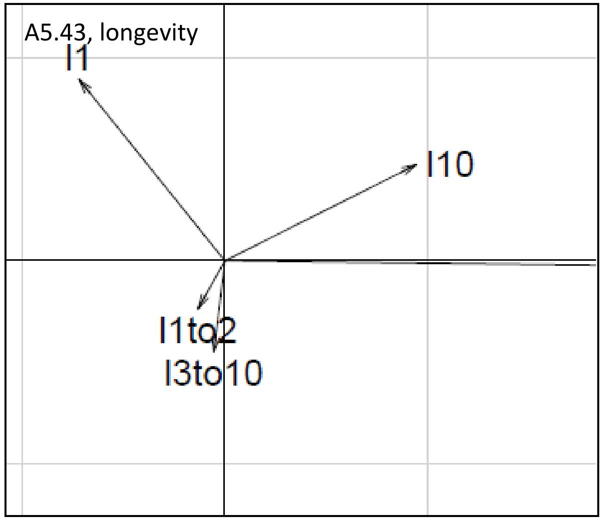

A5.35, longevity


A5.35, living habit
lhEpi
lhAtt
lhTube
lhFree
lhCrev
lhBurrow
A5.35, sediment position
spInf_10
spInf_0to5
spInf_6to10
spSurf
A5.35, bioturbation
bUpward
bSurf
bDiff
bDownward
bNone
A5.37, maximum size
sr10
sr201to500
sr11to20
sr101to200
sr21to100
A5.37, longevity
l1
l1to2
l3to10
l10
Trawling
A5.37, living habit
lhTube
lhBurrow
lhFree
lhEpi
lhCrev
lhAtt

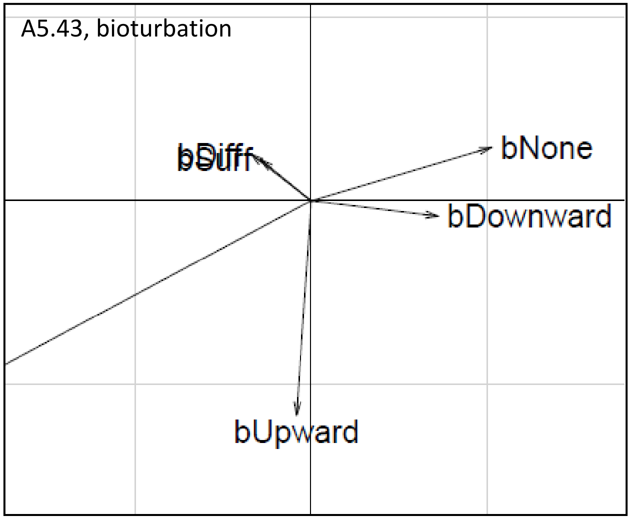

A5.37, feeding mode
fSurf
fPred
fScav
fSusp
fSub

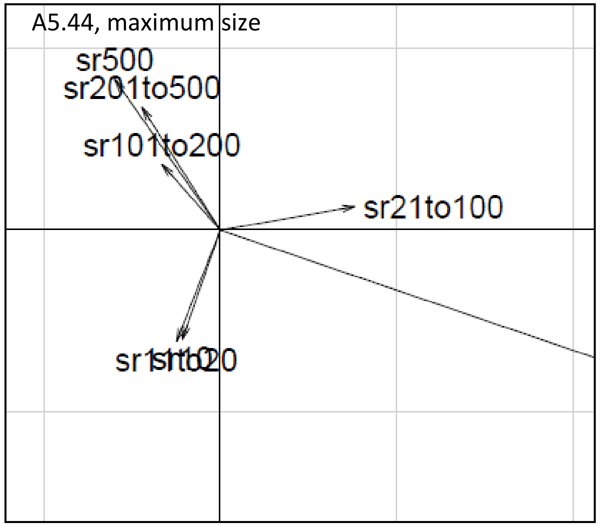

A5.37, mobility
mobSwim
mobSess
mobBur
mobCrawl

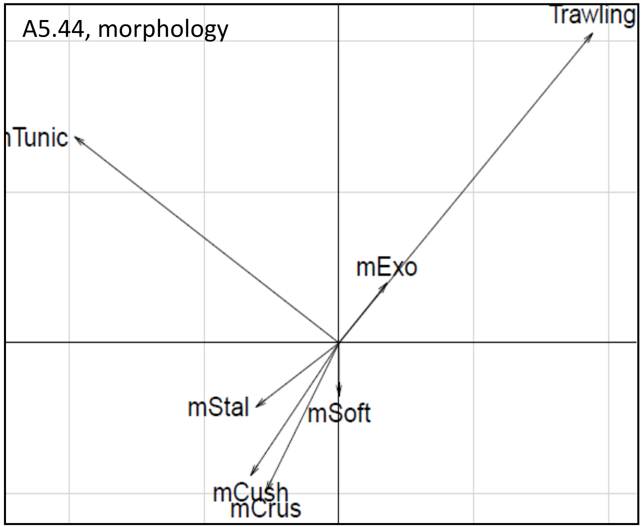

A5.37, bioturbation
bNone
bDownward
bSurf
bUpward
bDiff

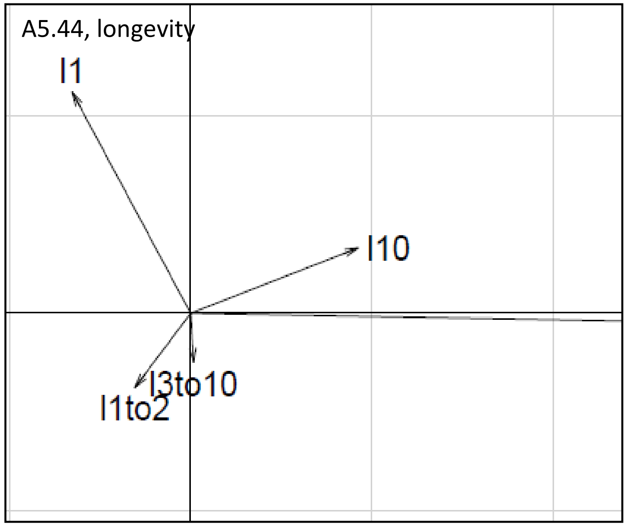

A5.43, longevity
l1
l10
l1to2
l3to10

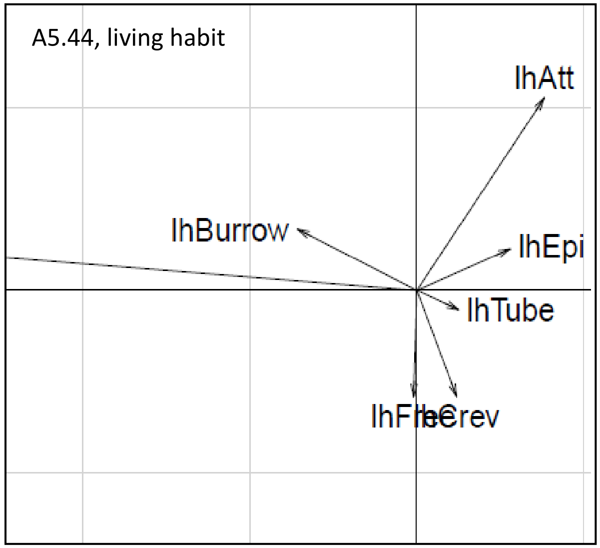

A5.43, egg development
edSex_pel
edAsex
edSex_br
edSex_ben

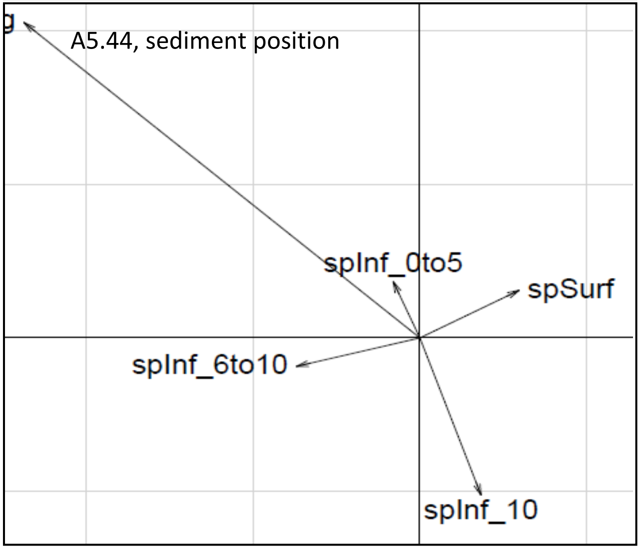

A5.43, bioturbation
bDiff
bSurf
bNone
bDownward
bUpward

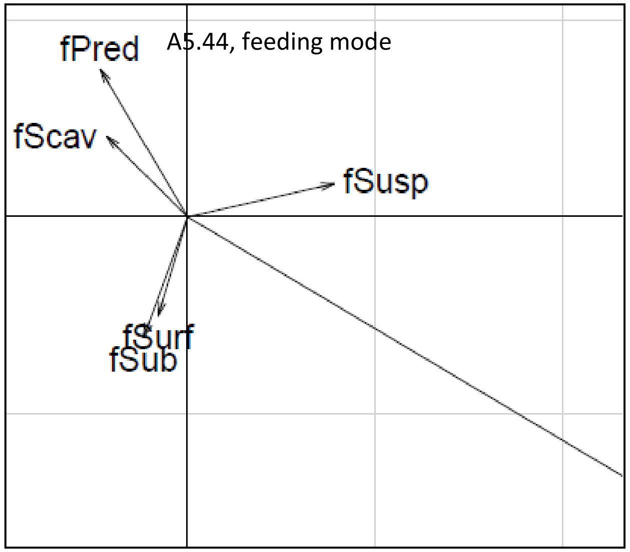

A5.44, maximum size

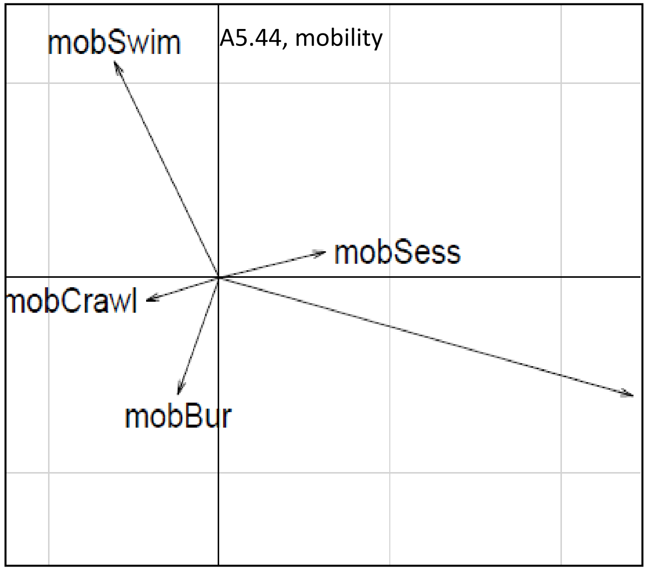

A5.44, morphology

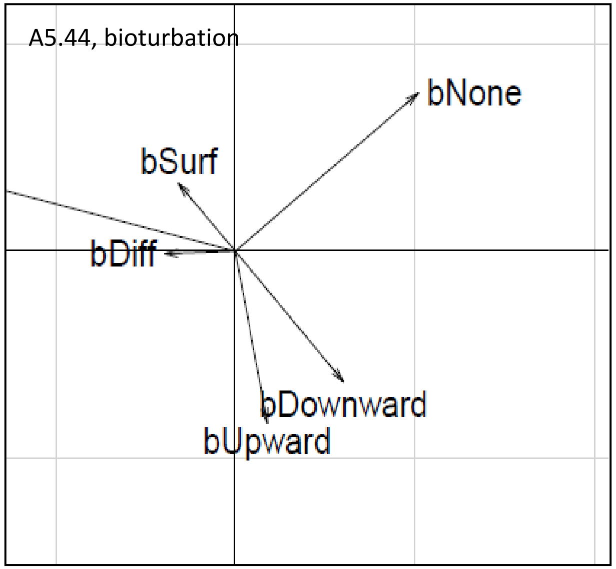

A5.44, longevity


A5.44, living habit

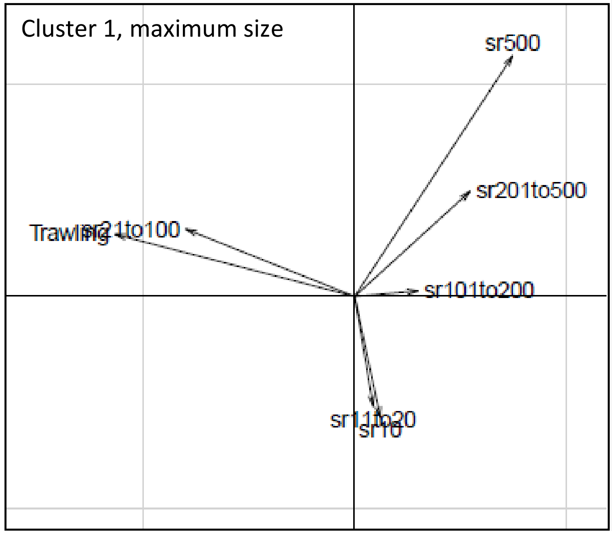

A5.44, sediment position

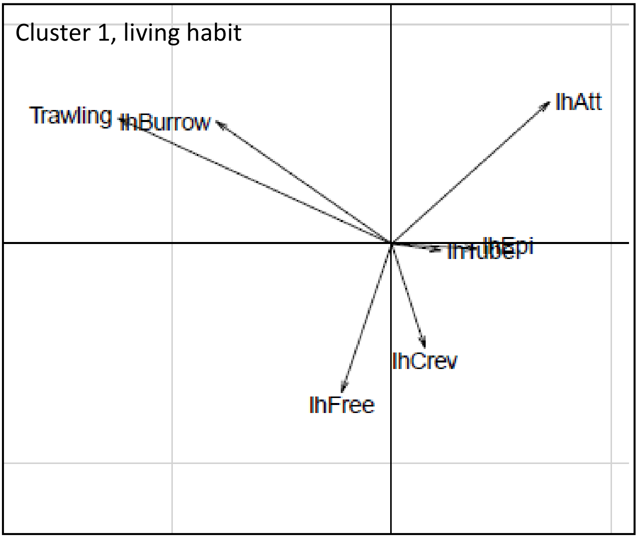

A5.44, feeding mode

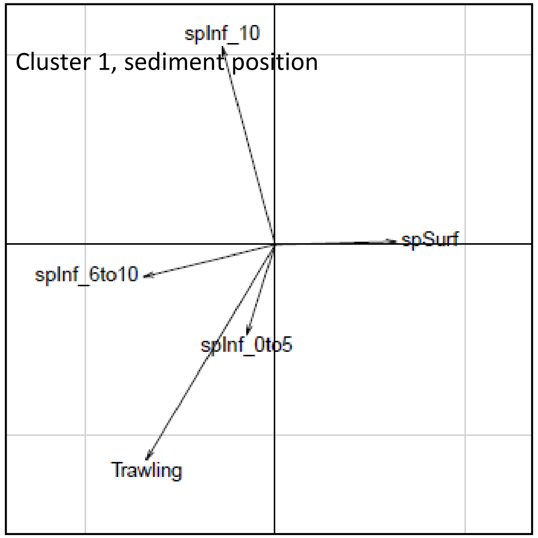

A5.44, mobility
mobSwim
mobSess
mobCrawl
mobBur

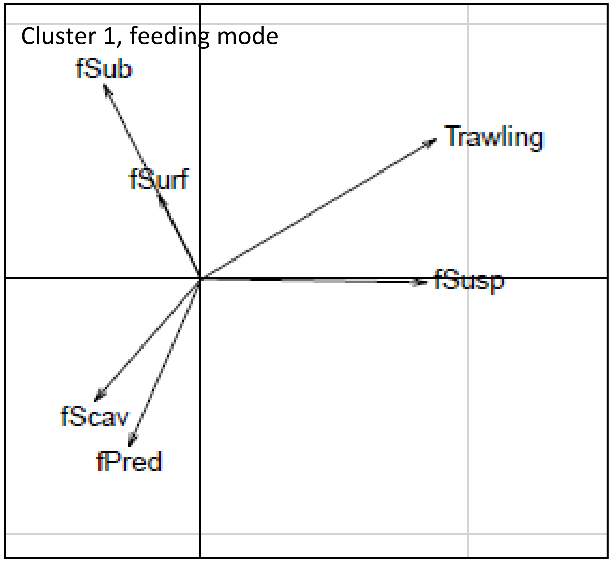

A5.44, bioturbation
bNone
bSurf
bDiff
bDownward
bUpward

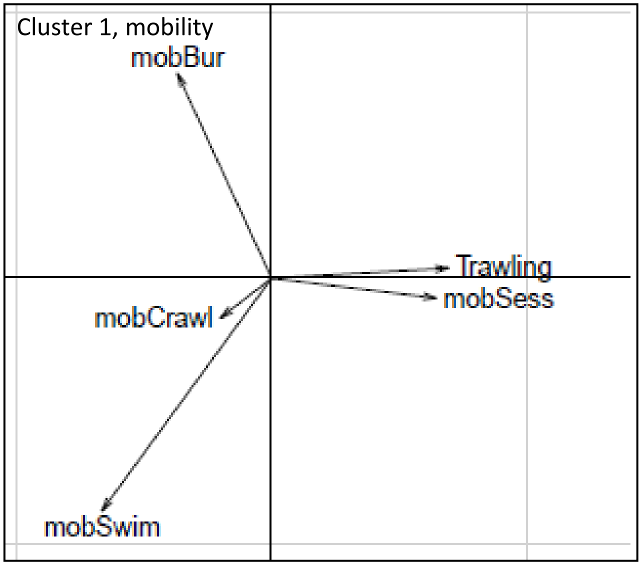
APPENDIX 2b: Infaunal stations by k-Means habitat clusters

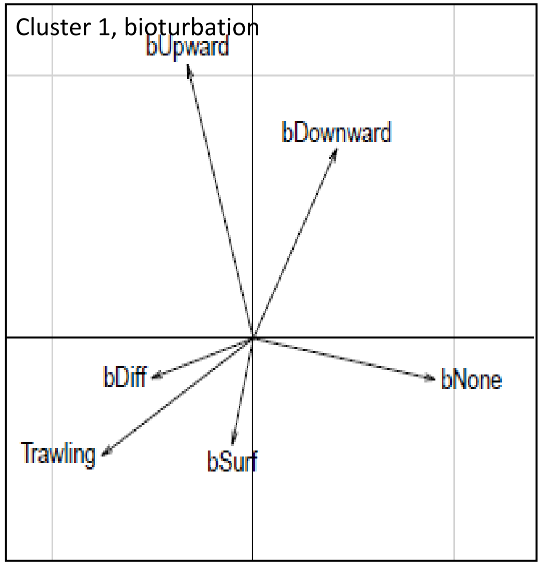

Cluster 1, maximum size
sr500
sr201to500
Trawling
sr21to100
sr101to200
sr11to20
sr10

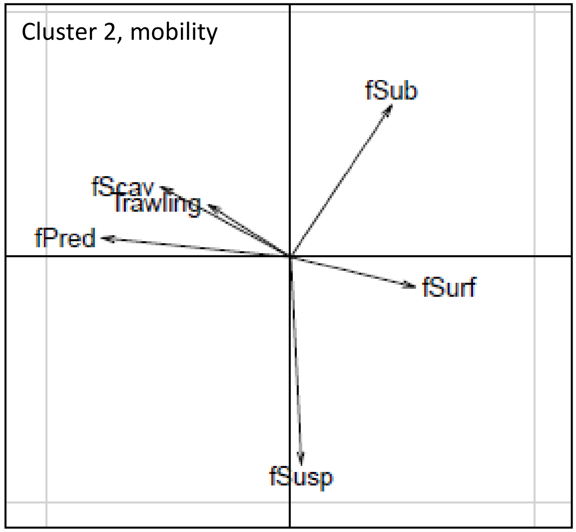

Cluster 1, living habit
Trawling
lhBurrow
lhAtt
lhTuber
lhEpi
lhCrev
lhFree

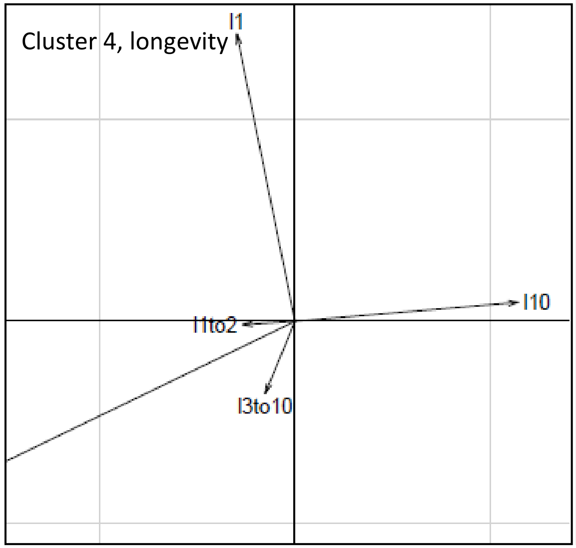

spInf_10
Cluster 1, sediment position
spSurf
spInf_6to10
spInf_0to5
Trawling

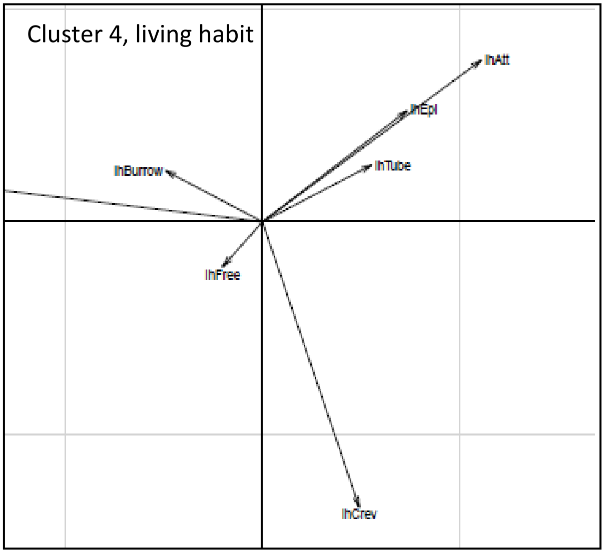

Cluster 1, feeding mode
fSub
Trawling
fSurf
fSusp
fScav
fPred

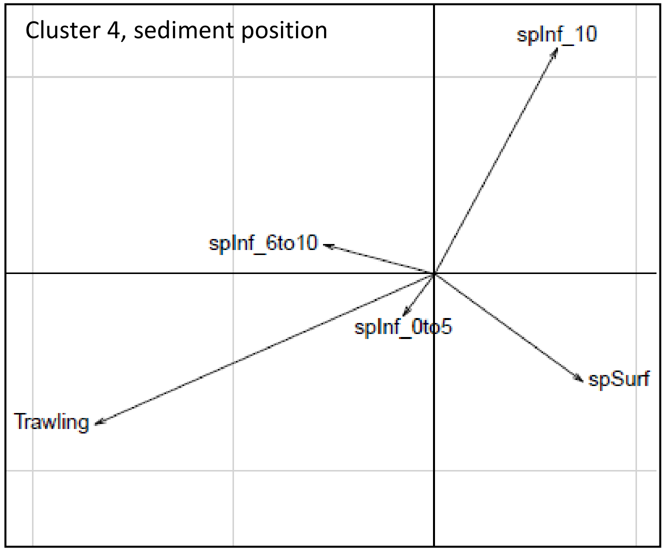

Cluster 1, mobility
mobBur
Trawling
mobSess
mobCrawl
mobSwim

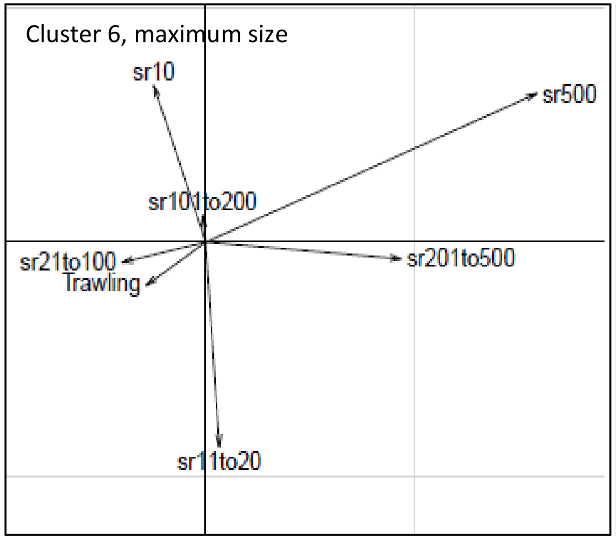

Cluster 1, bioturbation
bUpward
bDownward
bDiff
bNone
Trawling
bSurf

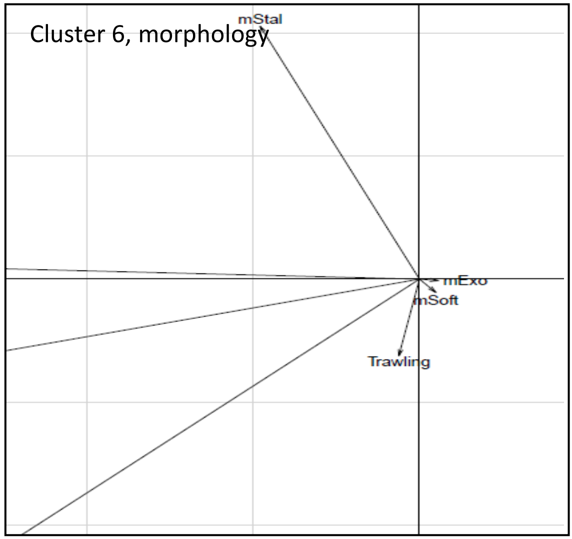

Cluster 2, mobility
fSub
fScav
Trawling
fPred
fSurf
fSusp

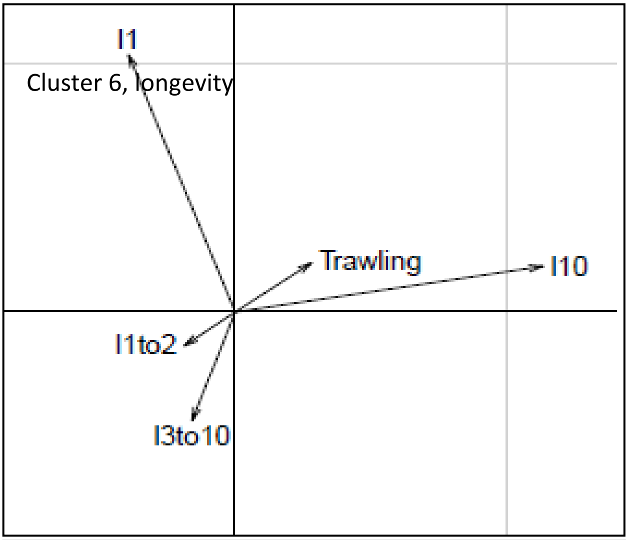

Cluster 4, longevity
l1
l10
l1to2
l3to10

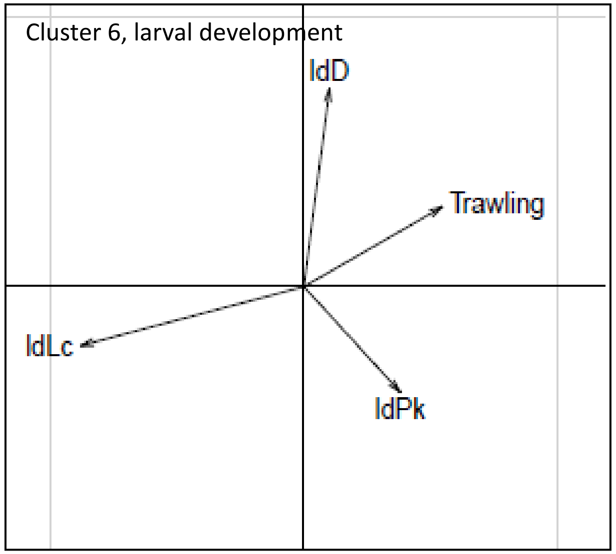

Cluster 4, living habit
lhAtt
lhEpi
lhTube
lhBurrow
lhFree
lhCrev

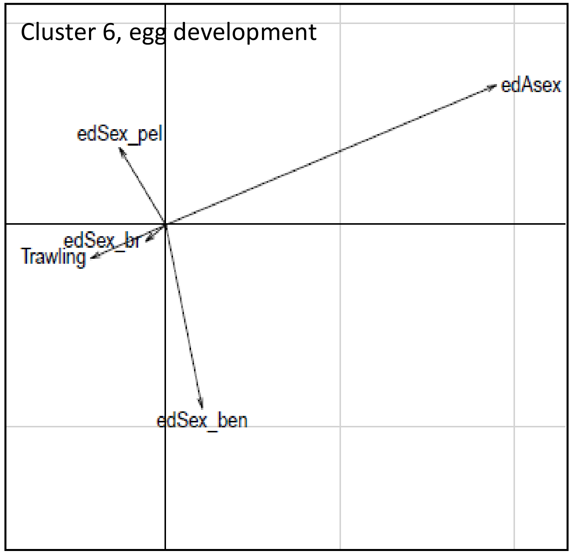

Cluster 4, sediment position
spInf_10
spInf_6to10
spInf_0to5
spSurf
Trawling

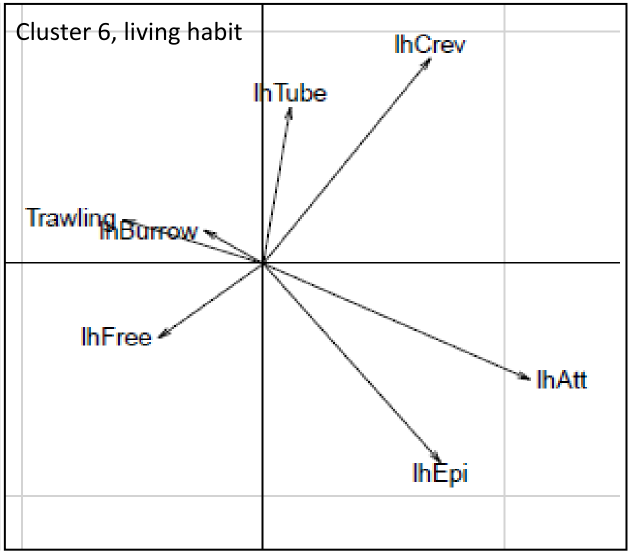

Cluster 6, maximum size
sr10
sr500
sr101to200
sr21to100
Trawling
sr201to500
sr11to20

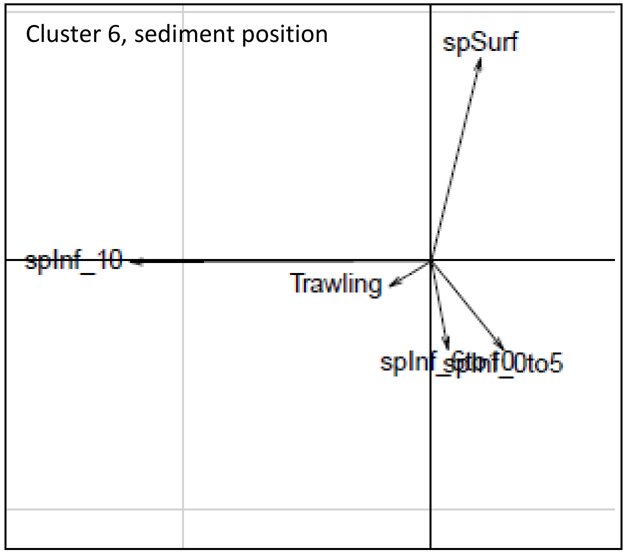

Cluster 6, morphology
mStal
mExo
mSoft
Trawling

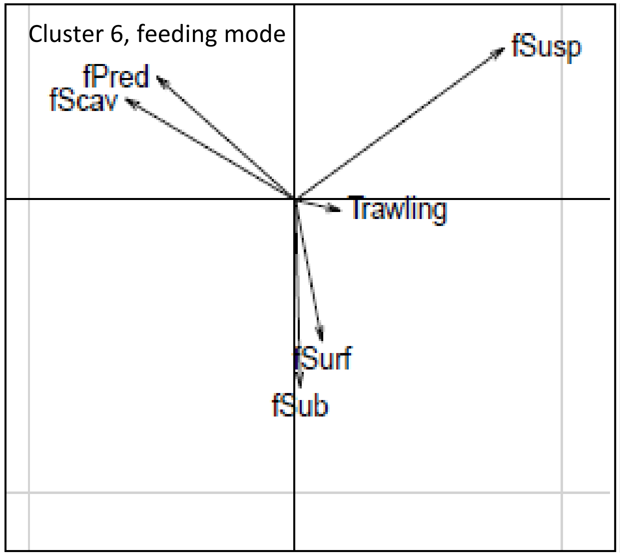

l1
Cluster 6, longevity
Trawling
l10
l1to2
l3to10

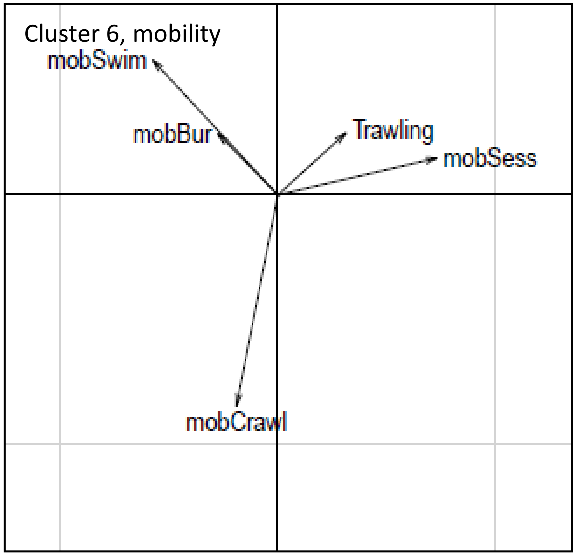

Cluster 6, larval development
ldD
Trawling
ldLc
ldPk

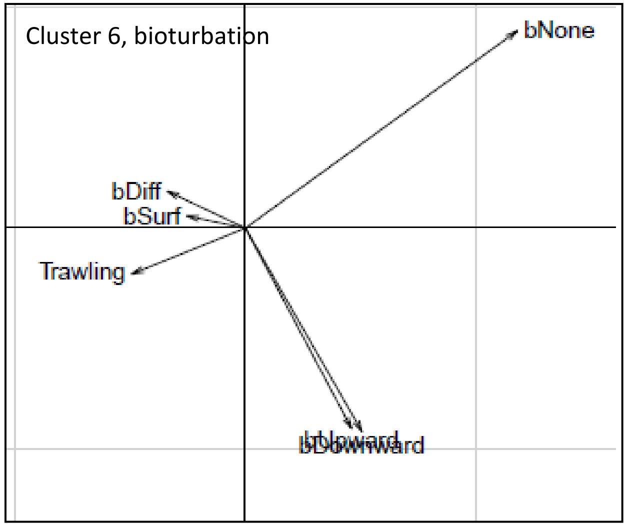

Cluster 6, egg development
edAsex
edSex_pel
edSex_br
Trawling
edSex_ben

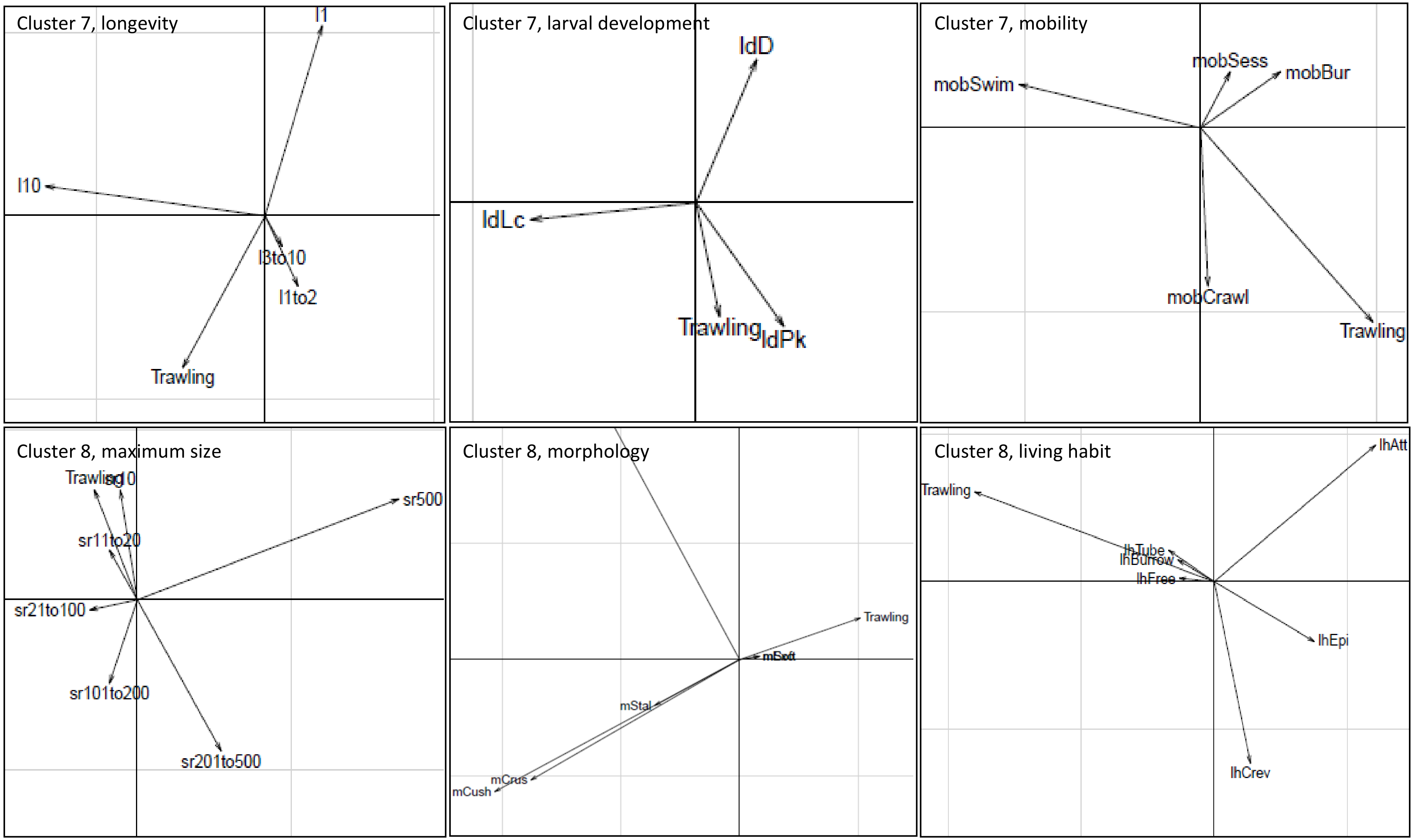

Cluster 6, living habit
lhCrev
lhTube
Trawling
lhBurrow
lhFree
lhAtt
lhEpi

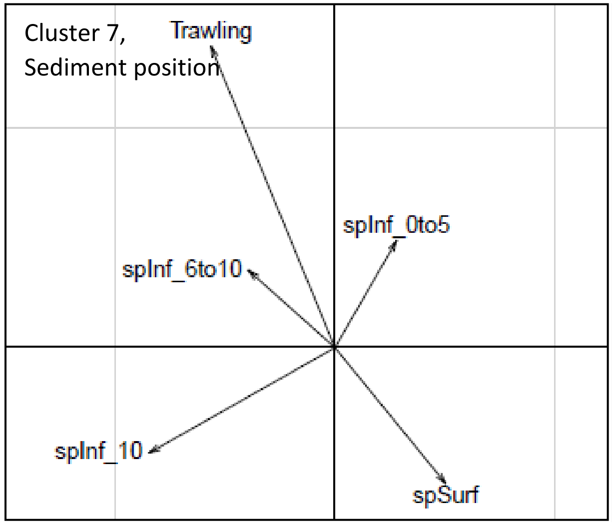

Cluster 6, sediment position
spSurf
spInf_10
Trawling
spInf_5to10
spInf_0to5

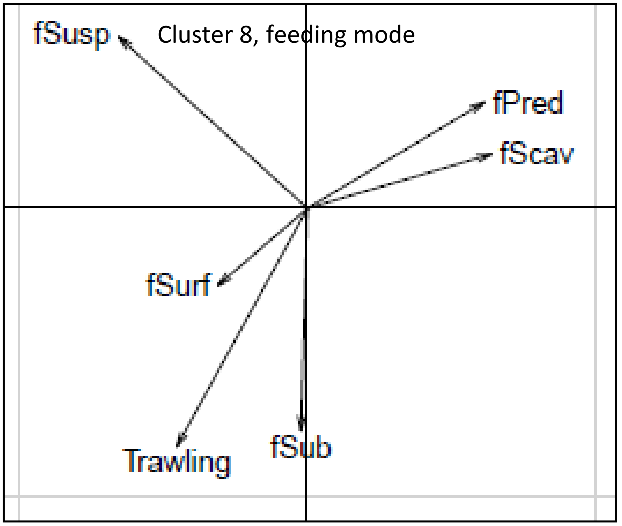

Cluster 6, feeding mode
fPred
fScav
fSusp
Trawling
fSurf
fSub

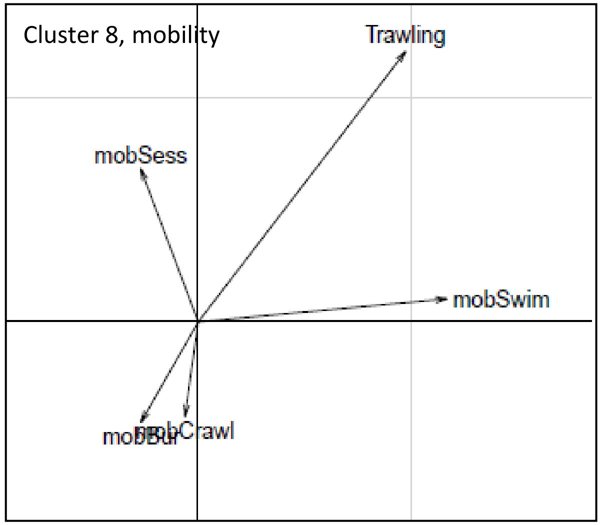

Cluster 6, mobility
mobSwim
mobBur
Trawling
mobSess
mobCrawl

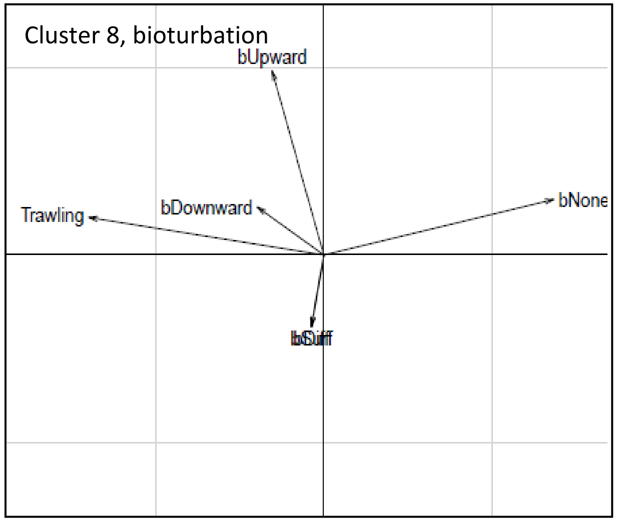

Cluster 6, bioturbation
bNone
bDiff
bSurf
Trawling
bUpward
bDownward


Cluster 7, longevity
l1
l10
l3to10
l1to2
Trawling
Cluster 7, larval development
ldD
ldLc
Trawling
ldPk
Cluster 7, mobility
mobSess
mobBur
mobSwim
mobCrawl
Trawling
Cluster 8, maximum size
Trawling
sr10
sr500
sr11to20
sr21to100
sr101to200
sr201to500
Cluster 8, morphology
Trawling
mSoft
mStal
mCrus
mCush
Cluster 8, living habit
lhAtt
Trawling
lhTube
lhBurrow
lhFree
lhEpi
lhCrev

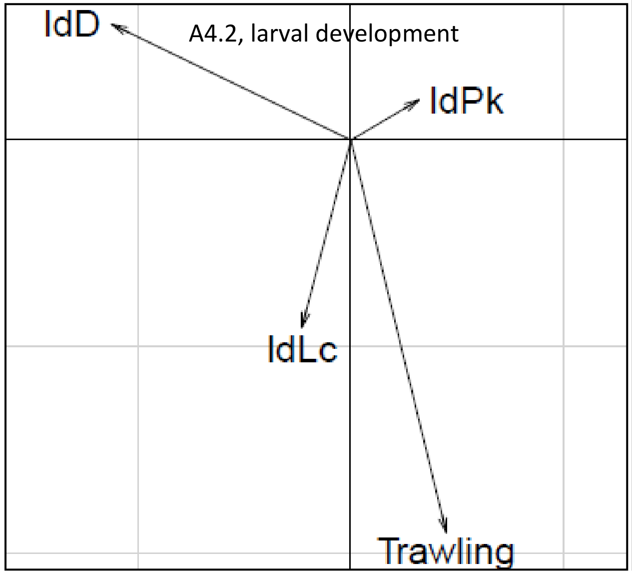

Cluster 7,
Sediment position
Trawling
spInf_0to5
spInf_6to10
spInf_10
spSurf

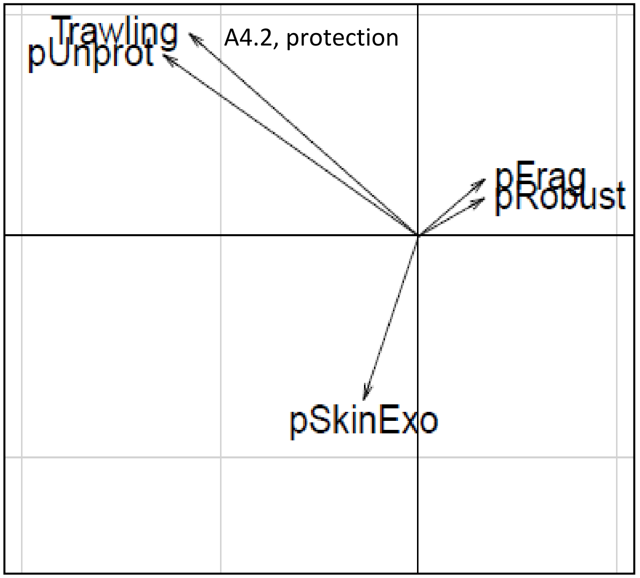

Cluster 8, feeding mode
fSusp
fPred
fScav
fSurf
Trawling
fSub

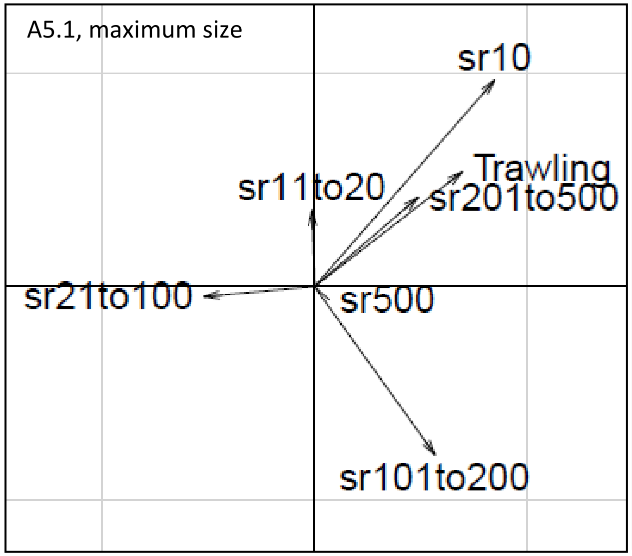

Cluster 8, mobility
Trawling
mobSess
mobSwim
mobBur
mobCrawl

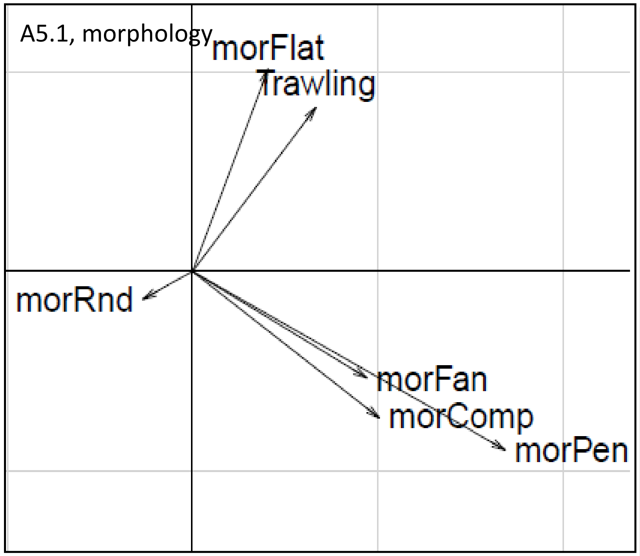

Cluster 8, bioturbation
bUpward
Trawling
bDownward
bNone
bSurf

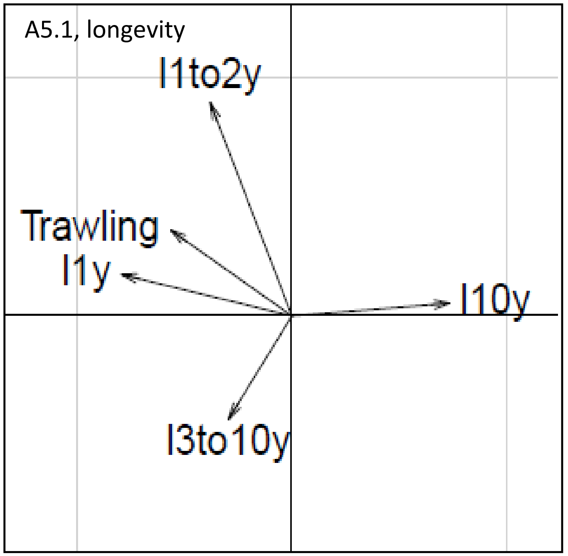
APPENDIX 2c: Epifaunal stations by EUNIS habitats

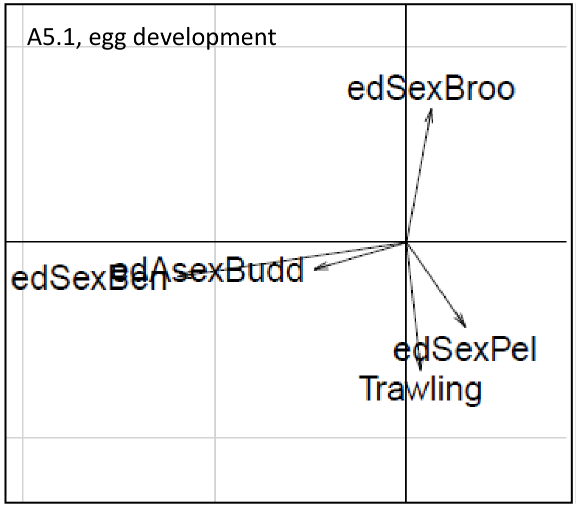

A4.2, larval development

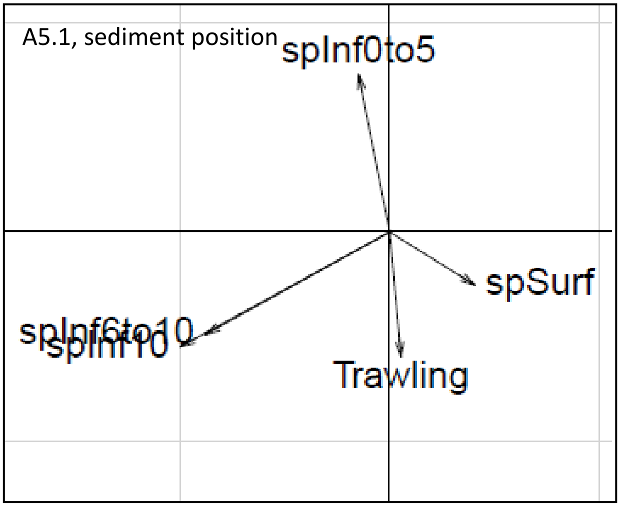

A4.2, protection

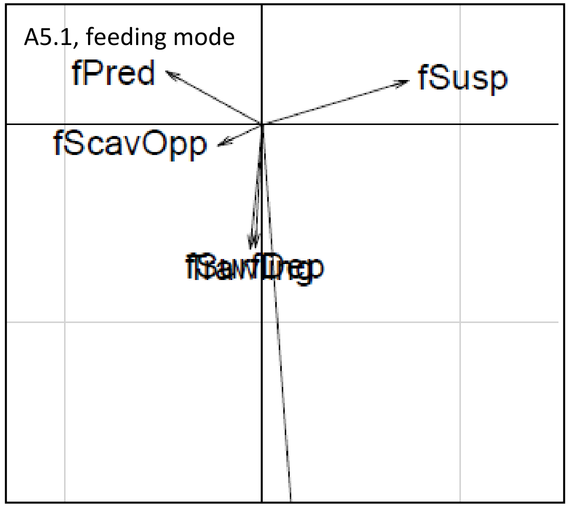

A5.1, maximum size

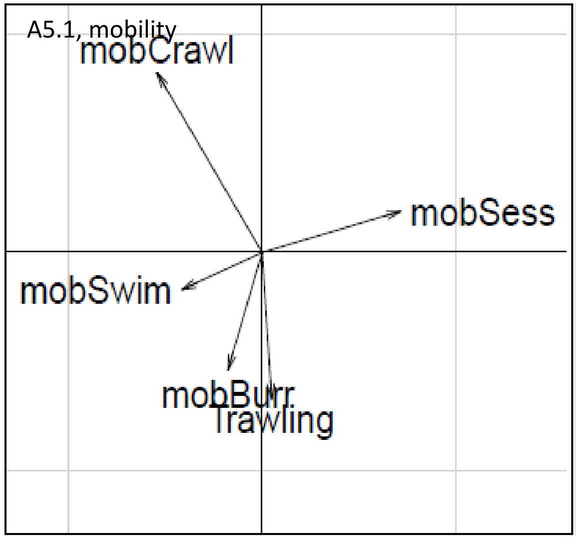

A5.1, morphology

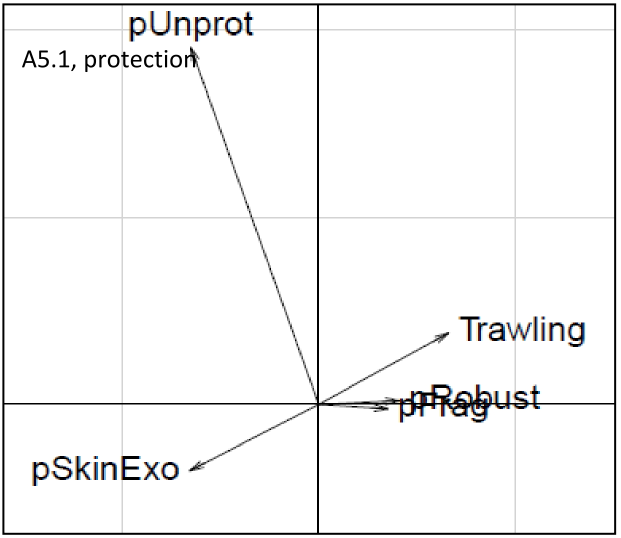

A5.1, longevity

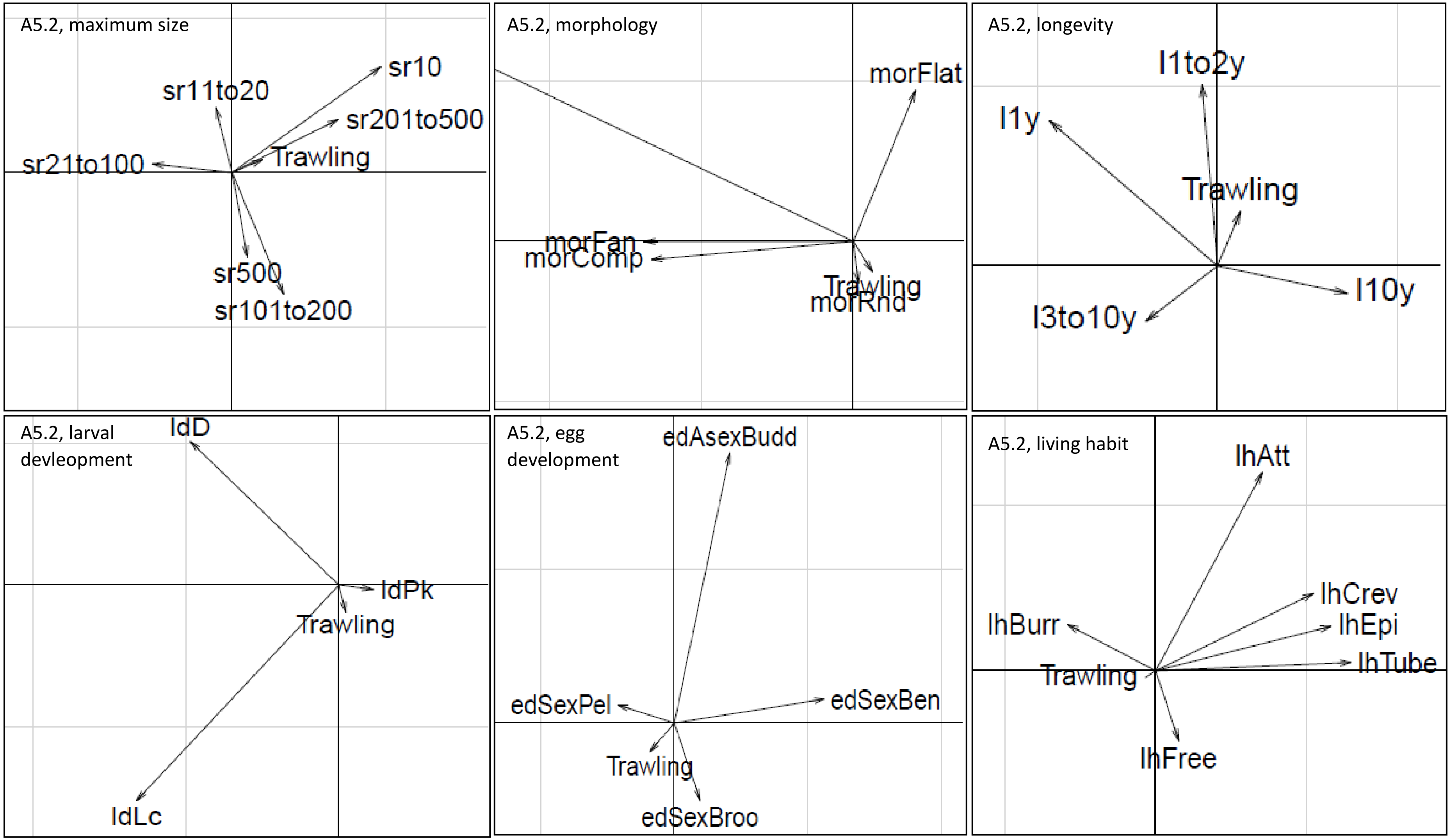

A5.1, egg development
edSexBroo
edSexBen
edAsexBudd
edSexPel
Trawling

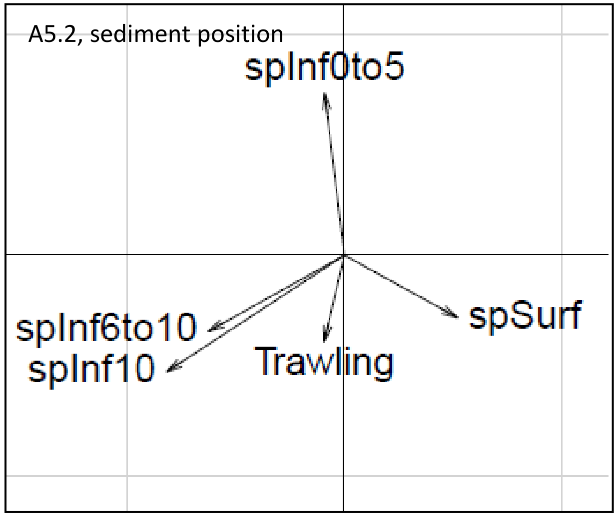

A5.1, sediment position
spInf0to5
spSurf
spInf6to10
spInf10
Trawling

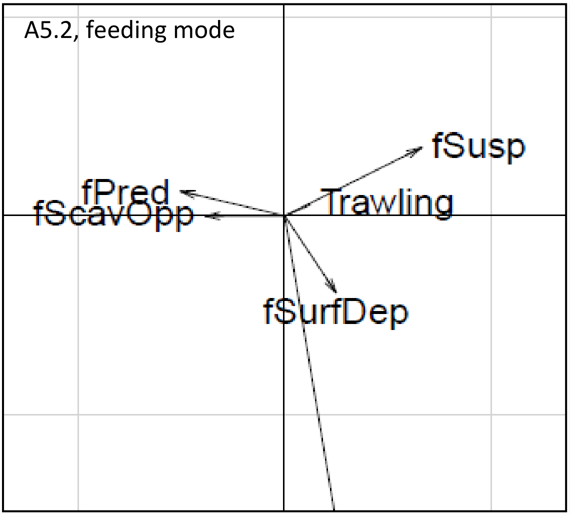

A5.1, feeding mode
fPred
fSusp
fScavOpp
fSurfDep
Trawling

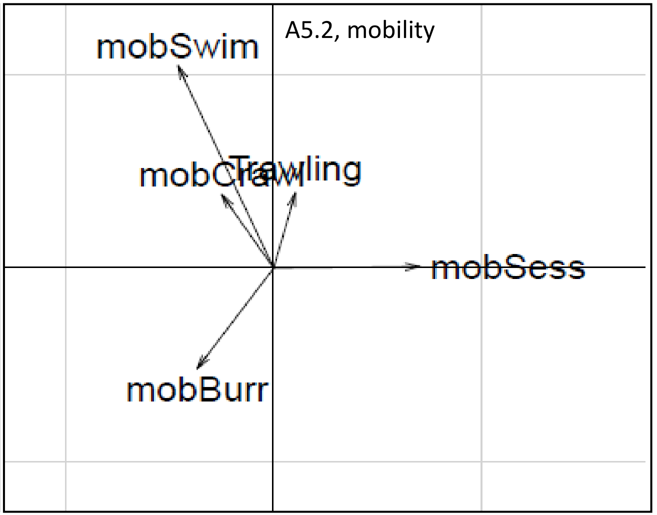

A5.1, mobility
mobCrawl
mobSess
mobSwim
mobBurr
Trawling

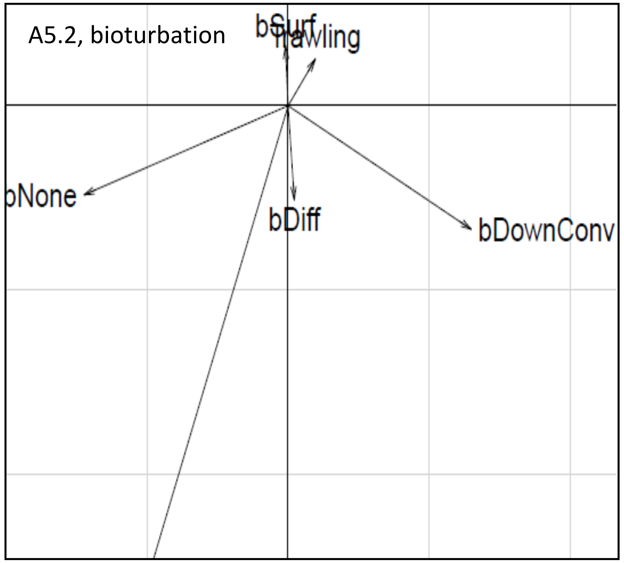

pUnprot
A5.1, protection
Trawling
pRobust
pFrag
pSkinExo

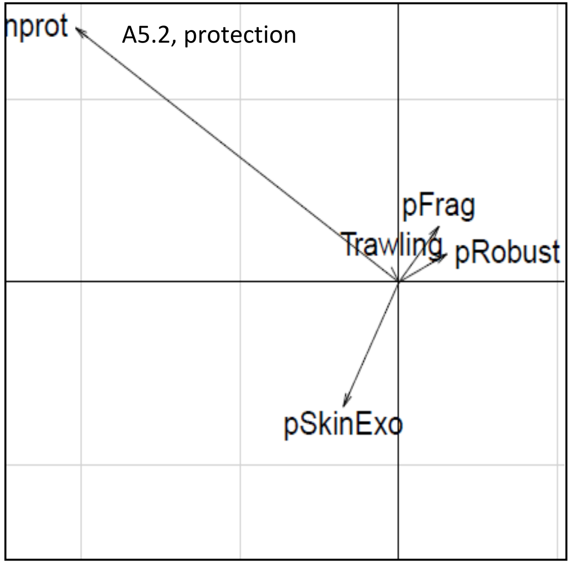

A5.2, maximum size
sr10
sr11to20
sr201to500
Trawling
sr21to100
sr500
sr101to200
A5.2, morphology
morFlat
morFan
morComp
Trawling
morRnd
A5.2, longevity
l1to2y
l1y
Trawling
l10y
l3to10y
A5.2, larval devleopment
ldD
ldPk
Trawling
ldLc
A5.2, egg development
edAsexBudd
edSexPel
edSexBen
Trawling
edSexBroo
A5.2, living habit
lhAtt
lhCrev
lhEpi
lhBurr
lhTube
Trawling
lhFree

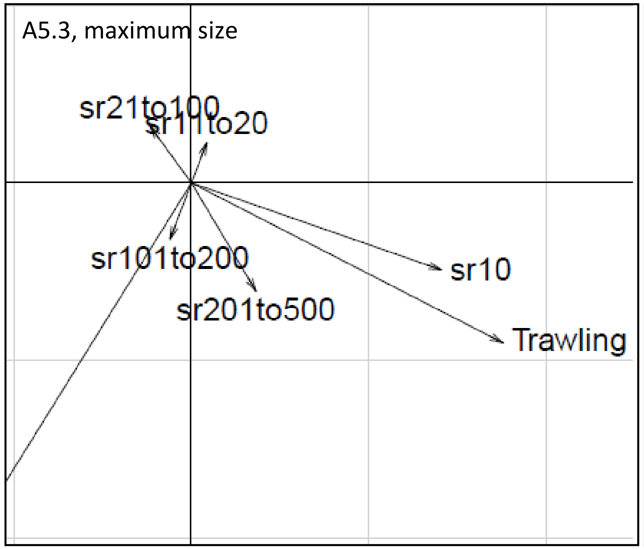

A5.2, sediment position
spInf0to5
spInf6to10
spInf10
Trawling
spSurf

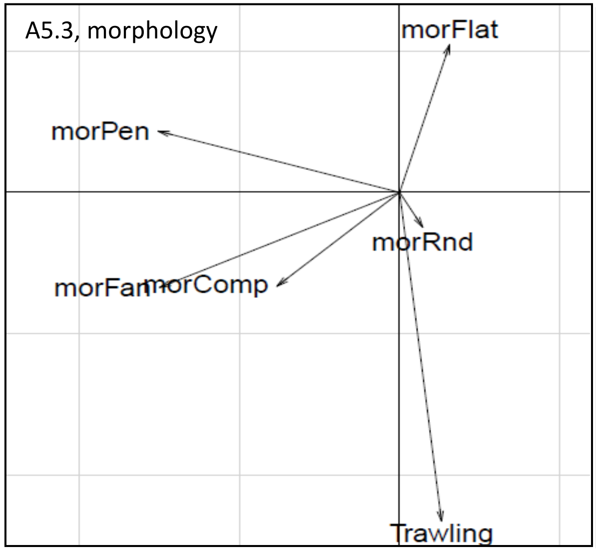

A5.2, feeding mode
fSusp
fPred
fScavOpp
Trawling
fSurfDep

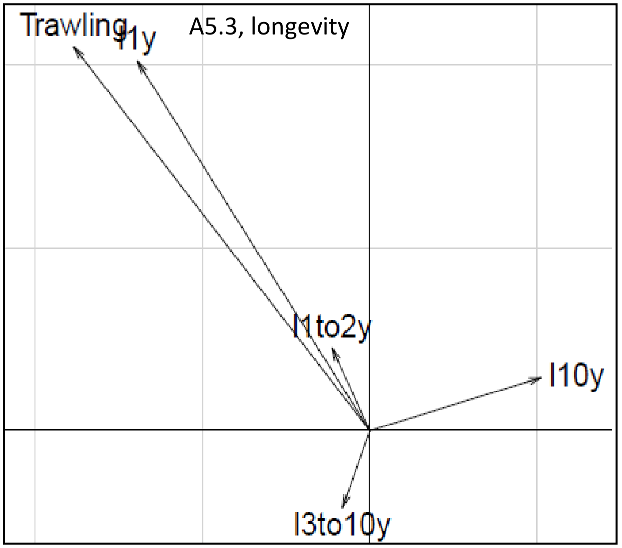

mobSwim
A5.2, mobility
mobCrawl
Trawling
mobSess
mobBurr

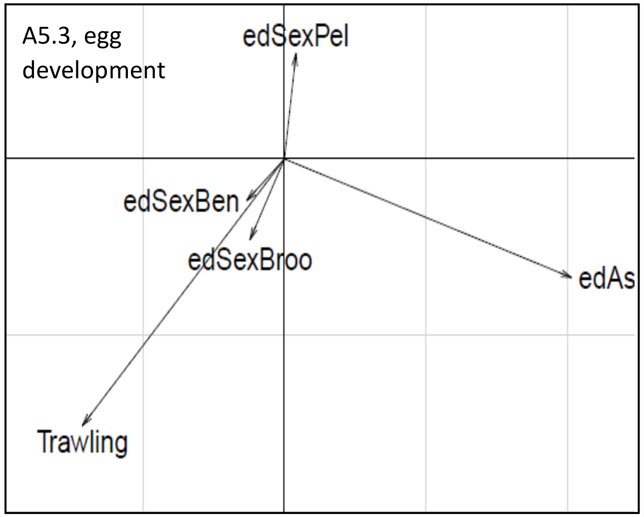

A5.2, bioturbation
bSurf
Trawling
bNone
bDiff
bDownConv

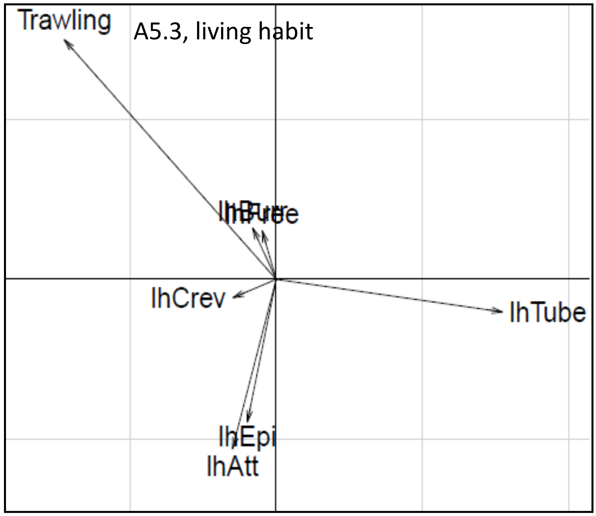

nprot
A5.2, protection
pFrag
Trawling
pRobust
pSkinExo

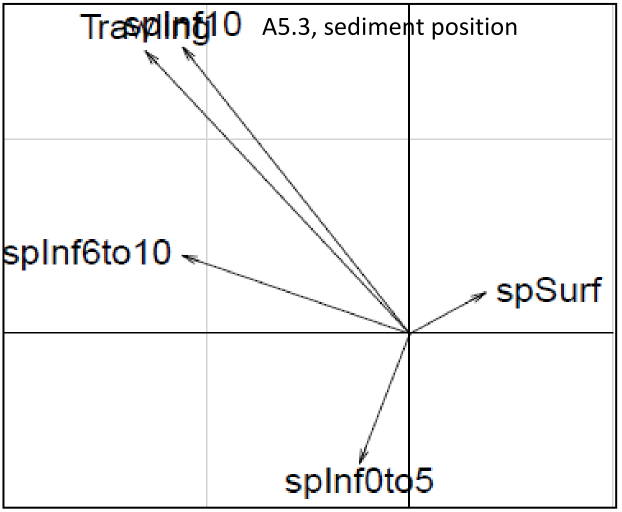

A5.3, maximum size
sr21to100
sr11to20
sr101to200
sr201to500
sr10
Trawling

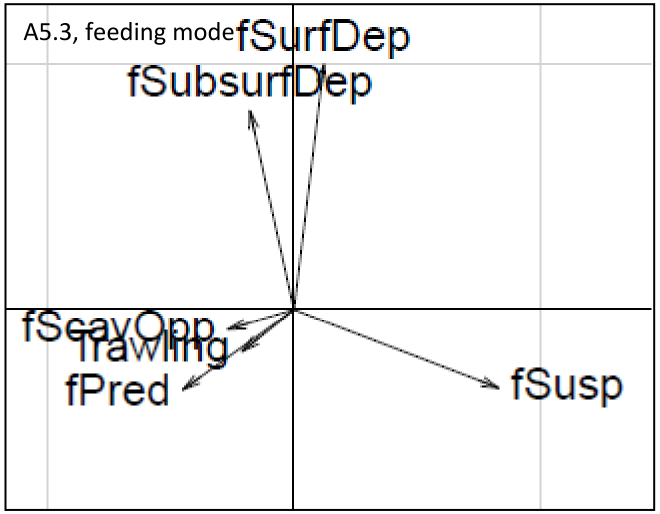

A5.3, morphology
morFlat
morPen
morRnd
morFan
morComp
Trawling

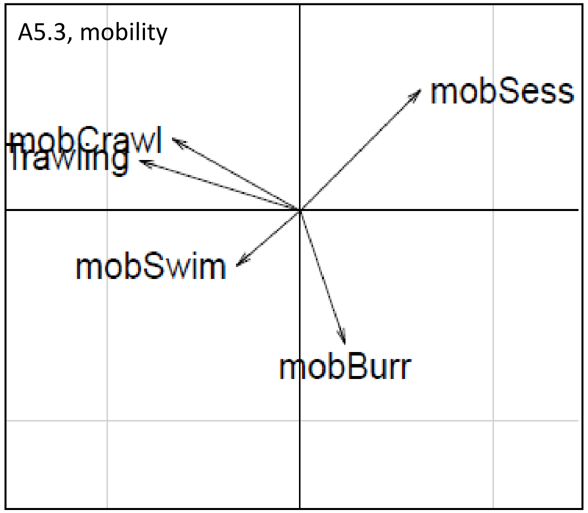

Trawling
l1y
A5.3, longevity
l1to2y
l10y
l3to10y

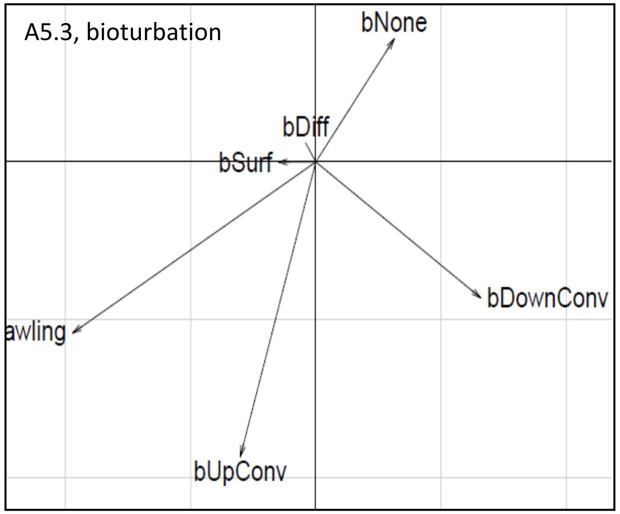

A5.3, egg development
edSexPel
edSexBen
edSexBroo
edAs
Trawling

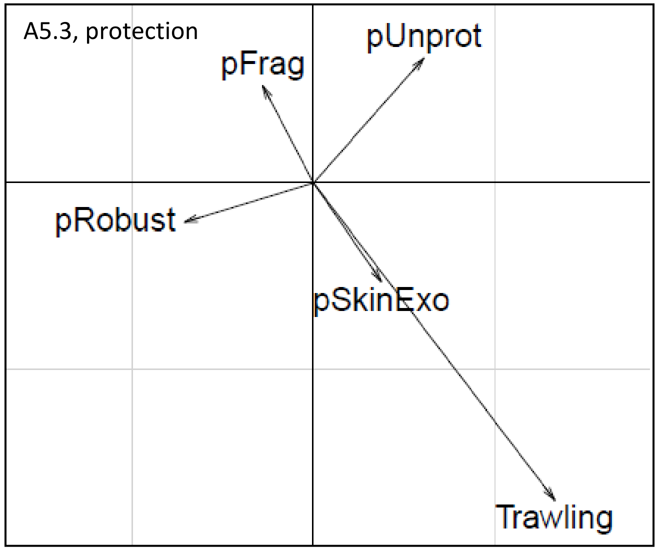

Trawling
A5.3, living habit
lhPure
lhFree
lhCrev
lhTube
lhEpi
lhAtt

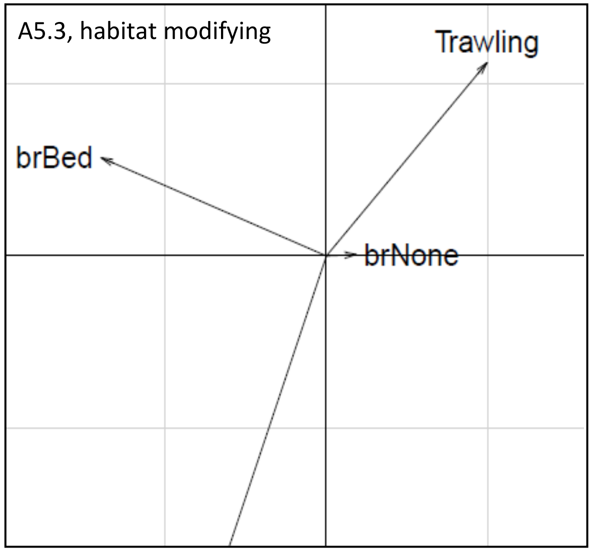

Trawling
spInf10
A5.3, sediment position
spInf6to10
spSurf
spInf0to5

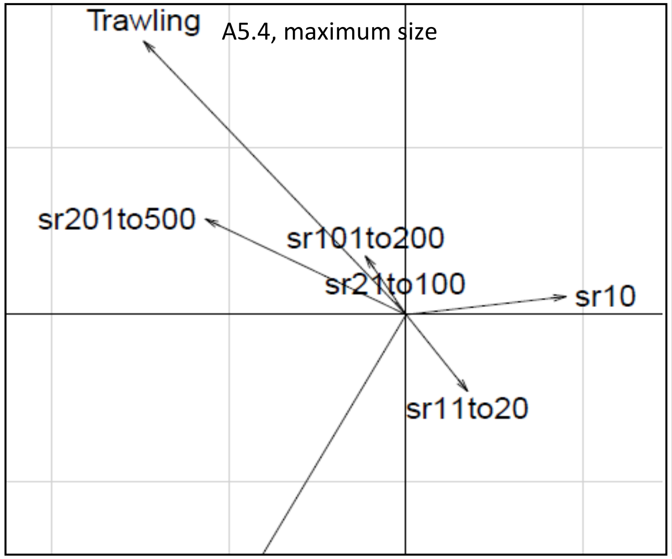

A5.3, feeding mode

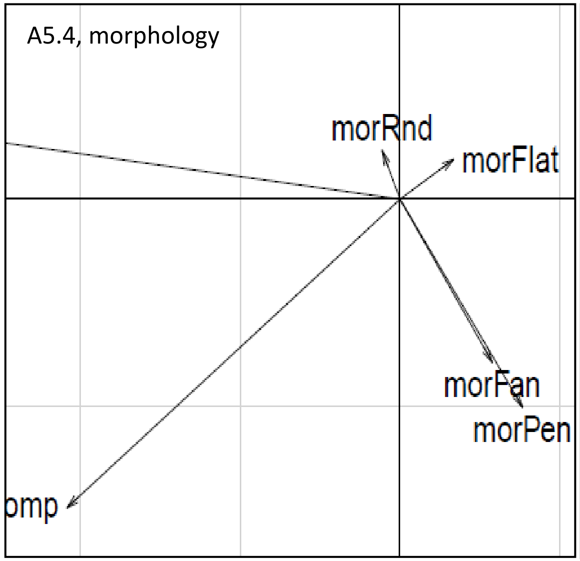

A5.3, mobility

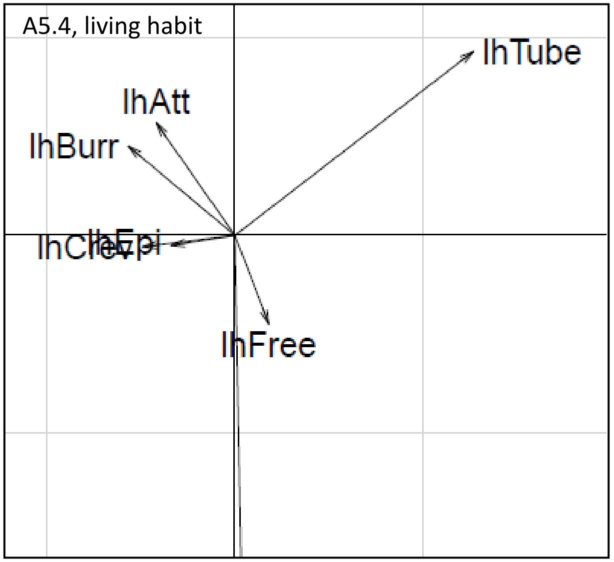

A5.3, bioturbation

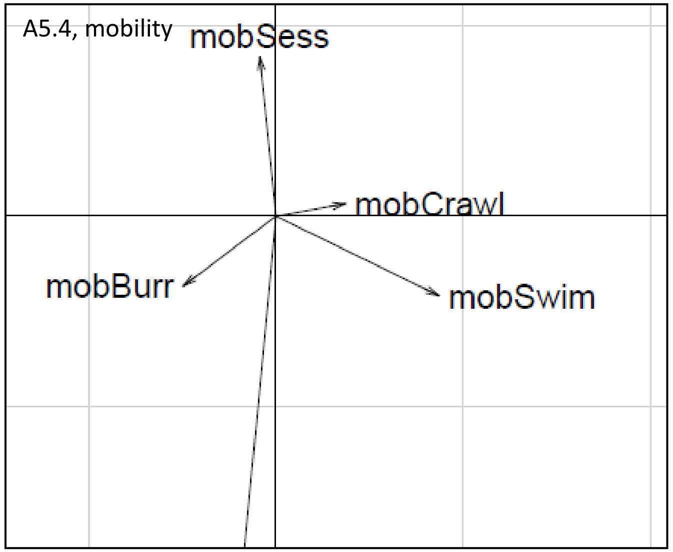

A5.3, protection

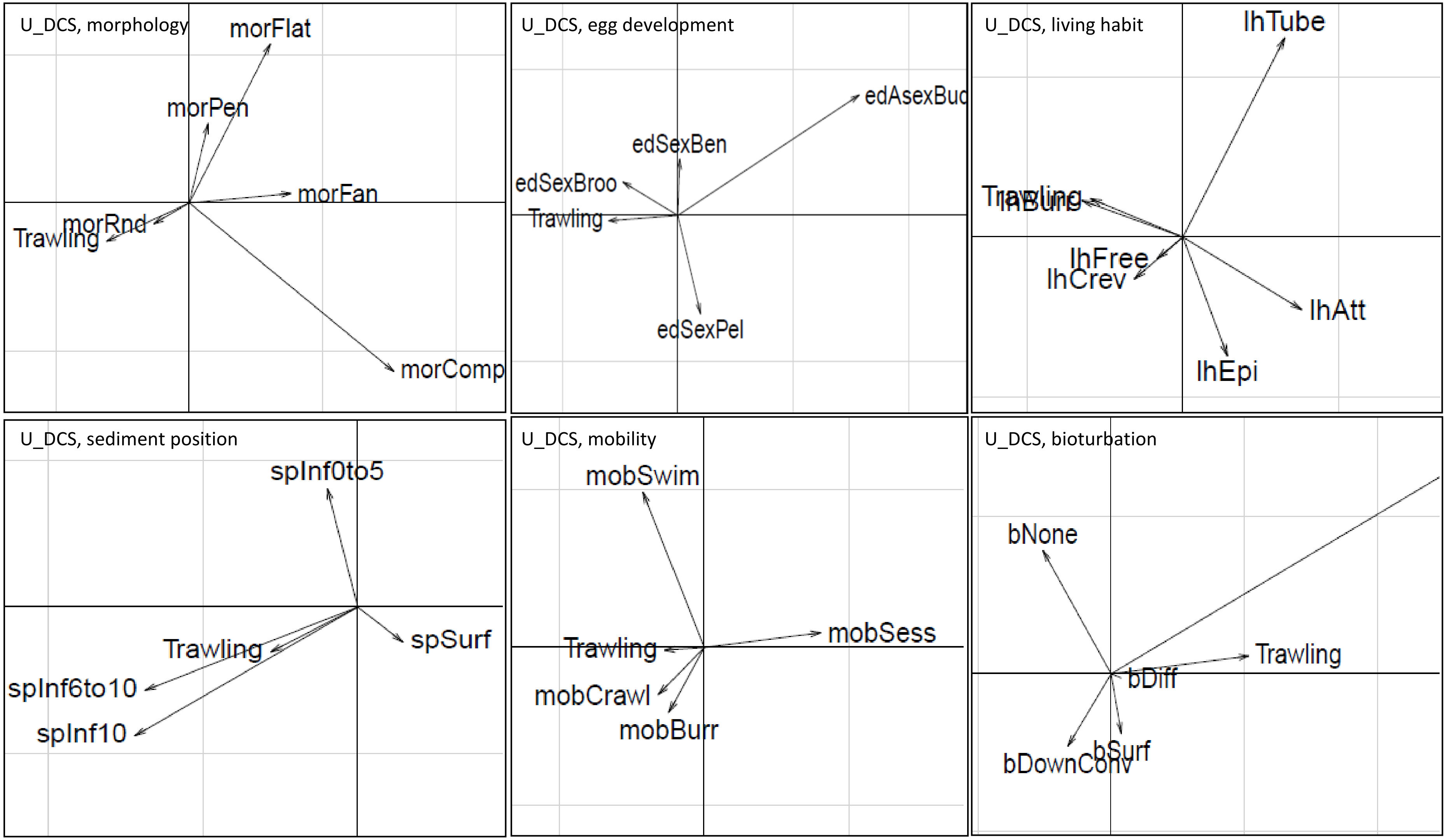

A5.3, habitat modifying

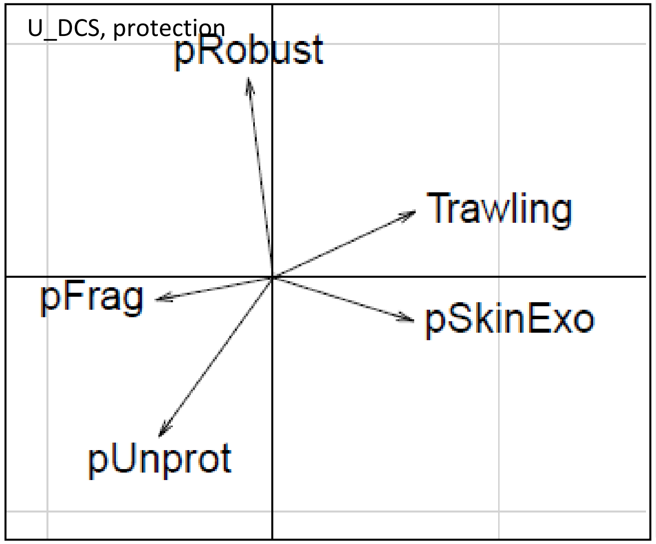

A5.4, maximum size
Trawling
sr201to500
sr101to200
sr21to100
sr10
sr11to20

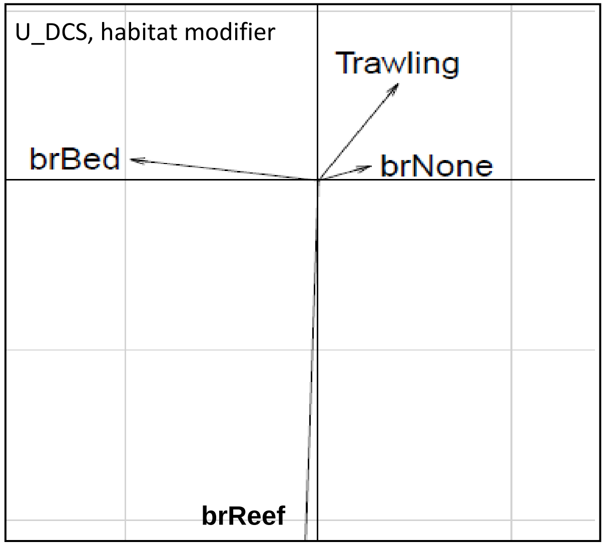

A5.4, morphology
morRnd
morFlat
morFan
morPen
omp


A5.4, living habit
lhTube
lhAtt
lhBurr
lhCrev
lhEpi
lhFree


A5.4, mobility
mobSess
mobCrawl
mobBurr
mobSwim


U_DCS, morphology
morFlat
morPen
morFan
morRnd
Trawling
morComp
U_DCS, egg development
edAsexBud
edSexBen
edSexBroo
Trawling
edSexPel
U_DCS, living habit
lhTube
Trawling
lhBurr
lhFree
lhCrev
lhAtt
lhEpi
U_DCS, sediment position
spInf0to5
spSurf
Trawling
spInf6to10
spInf10
U_DCS, mobility
mobSwim
mobSess
Trawling
mobCrawl
mobBurr
U_DCS, bioturbation
bNone
Trawling
bDiff
bDownConv
bSurf


U_DCS, protection
pRobust
Trawling
pFrag
pSkinExo
pUnprot


U_DCS, habitat modifier
Trawling
brBed
brNone
brReef